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A REVISION OF THE GENUS GORILLA.

BY

HAROLD JEFFERSON COOLIDGE, Jr.

WITH TWENTY-ONE PLATES AND TWO MAPS.

CAMBRIDGE, U. S. A.
Printed for the Museum.
August, 1929.

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A REVISION OF THE GENUS GORILLA.

By Harold Jefferson Coolidge, Jr.

INTRODUCTION.

Ever since Jeffries Wyman published his description of *Troglodytes gorilla* in 1847 in the Journal of the Boston Society of Natural History (Volume 5), large amounts of gorilla material have been accumulating in the museums of the world. Such eminent scientists as Richard Owen, Geoffroy St. Hilaire, A. Hrdlička, E. Selenka, Paul Matschie, Lord Rothschild, D. G. Elliot, and a host of others have studied this. At present there probably exist in the museums of the world some eight hundred gorilla skulls, counting adult males, females, and young. There are also skeletons, odd bones, and hides in far smaller quantities. With this amount of material it seems as though the time might at last have arrived when some conclusions of value could be drawn concerning the classification of these animals. In dealing with this subject attention has been repeatedly called to the fact that, as in other anthropoid apes, there is a very great individual variation in the gorilla. Nevertheless, from time to time new species and subspecies have been described, often on such a scanty basis as one or two specimens. As a result, one finds recognized today, and in current use in some museums, no less than fifteen different specific and subspecific names in the genus Gorilla. This does not include some of the earlier sporadic names that have since been regarded as synonyms. The difficulties of working up this gorilla material are largely due to the fact that it is so widely scattered in various museums, that the skulls other than those of adult males are of little use in determining classification, that the skulls are often broken, and that the region whence they come is often imperfectly or sometimes not at all known. These facts very considerably limit the number of specimens available for accurate scientific comparison. While not all the conclusions drawn in this paper can be claimed as final, it is hoped that the simplification of gorilla classification, found necessary as a result of exceptional opportunities for comparative study of existing material, may point toward a clearer conception of the way to meet future problems of classification in this important group. I make no attempt to belittle the magnificent work of scientists of the past in this field, but rather an effort to put facts together in a way that

many of them would have done themselves had they lived at a time when so much additional material was available for forming their final conclusions. The genus Gorilla, like many other genera of animals, has been through the usual stages of nomenclatural history and has at last reached the point where some sort of revision seems necessary. While this paper deals primarily with matters of skull variation and problems that arise from it, I hope to touch also on the matter of gorilla distribution in a very general way.

MATERIAL AND ACKNOWLEDGMENTS.

My interest in this problem was aroused by contact with the animals in the mountains of the eastern Congo while making zoölogical collections for the Harvard African Expedition (1927), under the leadership of Dr. Richard P. Strong. More than to anyone else I owe gratitude to Dr. Glover M. Allen of the Museum of Comparative Zoölogy at Harvard for his untiring assistance and inspiration. I also owe special thanks to Dr. W. L. H. Duckworth of Cambridge University, England, who helped me in my preliminary studies of gorilla material and put at my disposal his own collection. Acknowledgments for help are gratefully made to the following. In England: Forster Cooper; Dr. W. L. H. Duckworth, Cambridge University; Sir Arthur Keith, Royal College of Surgeons Museum; Oldfield Thomas, Captain Guy Dollman, M. A. C. Hinton, British Museum (Natural History); Dr. G. Elliot Smith; Dr. H. A. Harris; Anatomy School, London University; Major P. H. G. Powell-Cotton, Quex Museum, Birchington, Kent; Lord Walter Rothschild, Miss Hilda Jordan, Tring Museum. In Norway: Dr. A. Wollebach, Zoölogisk Museum, Oslo; Dr. K. E. Schreiner, Anatomisches Institut Kongelige Frederiks Universitet, Oslo. In Sweden: Count Nils Gyldenstolpe and Dr. Einar Lönnberg, Royal Natural History Museum, Stockholm. In Germany: Dr. E. Stresemann, Dr. Hermann Pohle, Professor Oscar Neumann, Rudolf Lips, Dr. Ernst Schwarz, Zoölogische Museum für Naturkunde, Berlin; Dr. E. Reichenow; Dr. Hans Schwann, Dr. B. Klass, Zoölogische Museum, Hamburg. In Holland: Dr. L. F. DeBeaufort; Dr. L. Bolk; E. Scheyder; P. G. Van Tienhoven, Zoölogisch Laboratorium, Amsterdam; Anatomisches Institut, Amsterdam; Dr. Van Kampen; Dr. E. B. Van Oort, Rijks Zoölogisch Museum, Leyden. In Belgium: Dr. H. Schouteden, Musée du Congo Belge, Tervueren; Dr. J. M. Derscheid. In France: Dr. J. Berlioz; Dr. G. Bourdelle; Dr. Bourret; Musée National d'Histoire Naturelle, Paris: Dr. M. R. Anthony, Anatomy Institute, Paris. In the United States: Dr. W. H. Osgood and S. C. Simms,

Field Museum of Natural History, Chicago; Gerrit S. Miller, Jr., United States National Museum, Washington, D. C.; Dr. Adolph H. Schultz, Johns Hopkins University, Baltimore; Dr. Witmer Stone, Academy of Natural Sciences, Philadelphia; Robert T. Hatt, James P. Chapin, American Museum of Natural History; Dr. Robert M. Yerkes, Institute of Psychology, Yale University; Dr. T. Wingate Todd, Western Reserve University, Cleveland; Dr. Thomas Barbour, Dr. Glover M. Allen, Miss H. M. Robinson, Museum of Comparative Zoölogy, Harvard College; Harold Jefferson Coolidge; Dr. E. Hooton; L. S. B. Leakey; T. Alexander Barnes; Dr. Dyce Sharp; J. F. Carrol; Dr. F. R. Wulsin; Dr. Joseph Bequaert; Miss Anna Hubbard; Miss Julia Curran.

METHODS.

Although gorillas are not necessarily confined to very limited regions through lacking means of locomotion or because of unsuitable environment, nevertheless they are at present found in two fairly restricted districts of equatorial Africa. Within these districts probably the only natural obstacles to their intermixing are mountains and rivers. Mountains, except when they are very much isolated, as in the case of the Kivu Volcanoes, have certainly not interfered with the wanderings of the gorilla. While we have as yet little evidence to show how much of an obstacle they find a river, a careful study of the accounts of those who know this animal in the field leads me to believe that it is not an insurmountable barrier. When we consider these facts, it seems improbable that there can be fifteen species or subspecies of gorilla within the two limited sections of Africa where they are found. On the other hand, it seems not unlikely that, as the two regions are separated by a forest belt of 750 miles width, some specific or subspecific difference might well appear to differentiate the gorillas of the two sections. To prevent confusion, I shall discriminate between the two sections by calling the one "mountain" and the other "coast." [1]

Reasons for Basing Classification Primarily on Male Skulls.

In the problem of classification there is no need to discuss the slight value of young or semi-adult skulls. The adult female gorilla skull, however, is often difficult to distinguish from that of a young male. In very few directions does the female seem to have carried her extremes of variation so far as the male.

Oppenheim (1911) has recorded the range of variation for fifteen different

[1] High mountains exist also in the interior of the coast region.

cranial characters in males and females of series of anthropoids. From these data the following figures were obtained.

In orang-utan skulls ten characters varied more extensively in males; five varied more in females. In chimpanzees only three of the fifteen characters showed a wider range in females than in males, and in the gorilla even, only one feature was less constant in the female. There are, however, on an average, five times as many cranial characters varying more in male than in female apes, than those which show a reversed relation (Schultz, Journ. Mamm., vol. 7, p. 192, 1926). The number of female skulls in collections is surprisingly small, and there seem to be many good reasons for basing the classification on the males.

A study of the skeletal parts of the male gorilla by Schultz has revealed a difference in hand, foot, and proportional length of limbs between Mountain and Coast Gorillas, but, of course, the available material is still rather limited for systematic study.

Pelage.

In dealing with the question of pelage and length and texture of hair, Gyldenstolpe (1928) suggests in his recent paper that the differences in color of fur may eventually prove to be merely phases of pelage attributable to age. He thinks that several of the alleged characters are valid for subspecific separation. In Elliot's Review of the Primates, a key to species and subspecies is published, in which this author lays emphasis on such characteristics as a chestnut patch on the head which he says is only found in the Cameroons. This key cannot be valid, because I have seen a Mountain Gorilla from west of Lake Kivu with a chestnut patch on its head. Lord Rothschild (1923) says that the Gaboon and Cameroons gorillas as distinguished from Mountain Gorillas are dimorphic in this respect. But it is safe to say that the male Mountain Gorilla has longer, thicker hair (also beard) than those from the coast. His principal color is a deep black with a gray or white area across the back. He occasionally has a sprinkling of gray or red hairs, usually on the crown of the head. There is also a characteristic callosity on the top of the head. The Coast Gorilla usually has shorter and thinner hair than the Mountain one, with no beard. He is often very gray and sometimes has a chestnut patch on his head and neck. He may be speckled with yellow as in the type of *Gorilla matschiei*. Beyond generalities we cannot go with the limited number of skins available for study, but it seems as if the greater length of hair in the Mountain Gorilla might have a subspecific significance if correlated differences are found in a systematic study of the adult male skulls.

Four Means of Studying Skulls.

My work on the adult male gorilla skulls may be roughly considered under four heads.

1. Literature.— A comprehensive reading and study of most of the available literature on the gorilla, with special emphasis on habits in the field that might affect the growth of its skull. Also a study of the writings on the gorilla's brain and skull by such anatomists as Anthony, Bolk, Duckworth, Elliot Smith, Selenka, Keith, and Harris, often supplemented by discussion of the subject with these men.

2. X-ray pictures.— A study of some X-ray pictures taken by Dr. H. A. Harris for the purpose of determining the endocranial form of gorilla skulls, with special reference to the existence of dolichocephaly (see Am. Journ. Phys. Anthrop., vol. 9, p. 157, 1926; also Proc. Zoöl. Soc. London, Sept. 29, 1927). Harris did pioneer work in this field and his study of fifty of Lord Rothschild's gorillas, in which he determined their radiographic endocranial ratios, has been of great value.

3. Scale photographs and methods of taking.— A comparative study of gorilla skulls was made by means of photographs. To do this I had a dozen black screens specially made and divided by white lines into centimeter squares. These screens were divided vertically and horizontally by two broader white lines which were used as a basis of orientation. The photographs were all taken with the greatest care. For the four views of each skull the screen was placed perpendicularly to the table on which the skull rested, one point of the skull always touching the screen, then the skull was oriented according to the following instructions: —

(*a*) The side view (*norma lateralis*) should be taken with the skull in the Frankfort plane.[1] Where possible the Frankfort plane should be along the same line as the horizontal base-line of the screen. The posterior point of the occipital surface of the skull should nearly touch the broad vertical white line on the left side of the screen.

(*b*) The front or facial view should be taken with the skull in the Frankfort plane. If possible the Frankfort plane should coincide with the horizontal base-line of the screen. It is most important that the vertical median line of the skull (from the prosthion or alveolar point to the summit of the crest) coincide with the vertical base-line of the screen.

[1] To be in the Frankfort plane the skull must have the true superior margin of the left and right external auditory meatus at the same level as the left infraorbital margin. It may be held in this position by a craniophore, by supporting it in a reversed position on three ordinary chemical-retort stands, or it may be supported by soft clay which can be blocked out from the photograph.

(*c*) The basal view (*norma basalis*) should be taken without the mandible. The median line of the skull should be along the horizontal base-line of the screen. The posterior point of the skull should be close to the broad vertical white line on the left side of the screen.

(*d*) The top view (looking down on the skull from above) should be taken with the median line of the skull along the horizontal base-line of the screen. The posterior point of the skull should be close to the broad vertical white line on the left side of the screen.

In all cases the skull was placed in such a good light that there was very little, if any, shadow, and, most important of all, the camera was set at such a distance from the object as to eliminate distortion (smaller than one-third natural size on the plate). Often a telephoto lens was used. As this photographing required time, skill, and a good deal of apparatus, I was unable to get photographs of all the skulls I wanted. However, I have a large series of over four hundred, for which I am especially grateful to the Berlin Museum, Hamburg Museum, Oslo Museum, Anatomy Museum at Amsterdam, Congo Museum at Tervueren, Lord Rothschild's museum at Tring, Major Powell-Cotton's museum, Dr. Duckworth's collection, and the Museum of Comparative Zoölogy. (Only my sudden illness prevented the Stockholm Museum from being on the list.) The material, when in this form, with the reference number on each picture, I find of great value. I can check all important measurements at a glance, and can make outline drawings of any parts of the skull that are of interest. Comparative studies are easily made if the skulls are all similarly oriented.

4. *Comparative Measurements.*— In most of the collections studied I have taken the following twenty-six measurements of the adult male gorilla skulls, in addition to having some of them photographed as just described.

1. *Greatest length* (gnathion to inion).— This is the longest dimension of the skull, exclusive of teeth.

2. *Zygomatic width.*— This is the greatest width of the skull, usually taken at the union of the jugal with the squamosal process.

3. *Cranial length* (glabella to inion).— This measurement is less important in gorillas on account of variable extension of the crest.

4. *Cranial width.*— Greatest width of brain case taken on the line of the intersection of parietal and squamosal sutures. The wall of the brain case is so thin at this point that such a measurement gives a fair approximation of the transverse diameter of the brain cavity.

5. *Cranial height.*— The distance between basion and point where sagittal crest forks in front. This gives approximate height of brain case.

6. *Orbital width.*— Distance across orbital cavities at inner border of fronto-jugal suture.

7. *Mastoid width.*— Measured slightly behind auditory meatus. Gives width across base of brain case. It is important in gorillas because of variation in shape of mastoid area.

8. *Height of occiput.*— Taken from upper border of foramen magnum to inion (Matschie calls this the height of the nuchal shield).

9. *Palatal length.*— Taken from anteriormost point of hind margin of palate to gnathion. This gives index to length of rostrum.

Three facial-triangle measurements: —

10. *Basal length.*— Basion to gnathion.

11. *Gnathion to nasion.*— Length of rostrum.

12. *Nasion to basion.*

Mandibular measurements: —

13. *Outside intercondylar width.*— Width across both mandibular condyles.

14. *Outside intercoronoid width.*— Width across both coronoids. These vary more than the intercondylar widths as they serve for muscle attachment rather than for articulation.

15. *Condylar width.*— Greatest transverse diameter of each condyle.

16. *Length of ascending process of ramus.* — The greatest anteroposterior length of ascending process of ramus taken slightly above the level of the molar crowns.

17. *Height of ascending process of ramus.*— Vertical height of a line passing through coronoid, perpendicular to the tooth row.

18. *Greatest width across jaws posteriorly.*

Tooth measurements: —

19. *Length of maxillary tooth row.*— From front of upper canine to back of third molar.

20. *Outside alveolar width, upper tooth row.*— Taken across alveoli of second upper molars. Gives distance across palate and tooth rows.

21. *Inside alveolar width, upper tooth row.*— Taken between second upper molars. Gives least lingual width.

22. *Length of mandibular tooth row.*— From front of lower canine to back of third molar. This corresponds to upper tooth row and is fairly constant.

23. *Mandibular width outside alveoli.*— Taken across second lower molars.

24. *Mandibular width inside alveoli.*— Taken between alveoli of second lower molars.

Special variation measurements: —

25. *Orbital arc using a base of 50 mm.*— Measures the height of an approximate section of the orbital ridge in the median line.

26. *Sagittal arc using a base of 50 mm.* — Measures height of a section of the sagittal crest in the transverse plane close to the posterior end of brain case and in front of lambdoid crest.

I have made no measurements of the nasals because I found so great an individual variation in length, width, and shape after examining the first fifty skulls, that it seemed without question to be a largely nebulous character. All the measurements mentioned have been taken on over two hundred adult male skulls. These and two hundred more, including a few female and semi-adult, have also been measured for asymmetry by taking the distance between the anteriormost point of the temporal fossa and the gnathion on the right and left side; also the distance from the mid-point of the posterior face of the mandibular condyle to the anterior median point of the jaw at the base of the incisors on the left and right sides. For comparison all the skull measurements have been reduced to percentages of the basal length. The skulls have been placed, according to the region of their origin, in the following broad groups: Gaboon (includes French Equatorial Africa and Spanish Guinea), Cameroons, Western Cameroons, Kivu Volcanoes, Eastern Mountain gorilla (other than those found on the Kivu Volcanoes), and gorillas of unknown locality. Where skulls have come from a definitely known localized region within these divisions they have been grouped together. Two separate curves of variation have been plotted for each measurement of the skulls from a given region. The first is an ascending curve, with the increasing percentages along the y line, which shows clearly the range of variation and the slope of the increase in variation. The second curve applies similarly to each measurement. Only the curves for the various regions have been plotted on the same graph. For instance, there is a graph of comparative palatal-length curves in which a separate curve represents each of the five regions. The x line has the percentages of the basal length and the y line the number of skulls. In this way one can compare the peaks of the curves and see their relation to one another, also whether they overlap one another enough so as to make what might be specific differences into subspecific differences. There may sometimes be differences of but slight importance between certain groups or in certain measurements. Taking the average of the peaks of all these curves, one can determine a normal for existing skulls.

By study of measurements, curves, percentages, X-ray and scale photographs, literature, and the skulls themselves, I have reached the conclusions given at the end of this paper.

CLASSIFICATION.

Geographic Grouping.

I shall discuss classification as if it were an entirely new problem and try not to be prejudiced by previous work on the subject. For purposes of comparative systematic study it is necessary to adopt some system of grouping skulls according to their geographic distribution. The gorillas of the West Coast region seem naturally to group themselves into three major geographical divisions: (1) the Western Cameroons, which is a comparatively limited section centering around Mamfe or Dakbe and extending west as far as the Cross River. A great many skulls come from this region and they have mostly been classified as *Gorilla gorilla diehli* by Matschie. (2) Cameroons: this division centers around Yaunde. (3) Gaboon, which should include Spanish Guinea. The majority of the Gaboon skulls have come out from the region of the Ogowe River. (A large number of the skulls in the various collections have no more definite marking than Gaboon, Cameroons, West Cameroons.) East of the Gaboon we have a stretch of forest in French Equatorial Africa centering around Wesso. The skulls from this region often came out through the Gaboon and so were called Gaboon gorillas, but since it is so hard to be certain which are the true Gaboon ones and which are from French Equatorial Africa in the same forest but farther east, I have called the whole group the Gaboon gorilla in making my study of classification. As far as possible I have grouped the skulls from these three large regions into smaller groups to include only those coming from more limited areas, so that in making comparative curves of different measurements, any single group from a limited area that showed possible subspecific peculiarities would immediately attract attention when otherwise its traits might be obscured in the general average of the larger district.

In the mountain regions the gorillas of the Kivu Volcanoes seem to be somewhat isolated from those of the other mountain ranges that run north and south in eastern Congo. There have been recent volcanic disturbances in the Kivu region and possibly this may have had something to do with cutting off the volcanoes of the west from the adjoining mountain forest or, more likely, the once continuous forest has since been interrupted in this region. For purposes of study it seems wise to group the gorillas found among the Kivu Volcanoes and on the

eastern slopes of the adjoining mountains that run down into Uganda, all under the heading of Kivu gorillas. Along the ranges running north and south in the eastern Congo we find gorillas. The southern limit is in the mountains west of Lake Tanganyika, not far from the north end of the lake. Scattered troops that seem to wander for considerable distances are found from here up to the north of Lake Edward. They all occupy the same long range or chain of mountains and usually are in the forests that cover the higher parts of these ranges above the line of bamboos (from 7,000 feet up). It seems best to group all these gorillas together, as no natural barriers divide them, and to call the group the Eastern Mountain gorillas. Then there remains a last but large group of gorillas coming from unknown localities. Their skulls are only of value in making a study of variation and of little help in classification.

To sum up, I have considered the *Coast* skulls under three groups, viz., those from the West Cameroons, Cameroons, and Gaboon; and the Eastern Congo or *Mountain* skulls under two groups, Kivu and the Eastern Mountain gorillas. With this grouping a systematic study of the skull measurements follows.

Skull Measurements of Gorillas.

In the table following are given the skull measurements of 213 adult gorillas, as made by the writer in the course of this study.

Abbreviations.

Various museum collections: —

A.M.N.H.	American Museum of Natural History, New York, New York.
Amst.	The Anatomical Institute, Amsterdam, Holland.
Anat. P.	Anatomy Institute, Paris, France.
Berlin	Zoologische Museum für Naturkunde, Berlin, Germany.
Brit. M.	British Museum (Natural History), London, England.
Cambr.	Duckworth collection, Cambridge University, England.
Field	Field Museum of Natural History, Chicago, Illinois.
Hamb.	Zoologische Museum, Hamburg, Germany.
H. C.	Personal collection of writer.
Leiden	Rijks Zoologisch Museum, Leiden, Holland.
M.C.Z.	Museum of Comparative Zoölogy, Harvard University, Cambridge, Mass.
Oslo	University Anatomy Institute, Oslo, Norway.
Paris	Musée d'Histoire Naturelle, Paris, France.
Quex	Major Powell-Cotton's collection, Quex Museum, Birchington, Kent, England.
R.C.S.	Royal College of Surgeons Museum, London, England.
Stock.	Royal Natural History Museum, Stockholm, Sweden.
Tervueren	Musée Congo, Tervueren, Belgium.
Tring	Lord Rothschild's Collection, Tring Museum, England.
U.S.N.M.	United States National Museum, Washington, D. C.

Geographical Grouping: —

Cam.	Cameroons (all except western part).
E. Mt.	Mountain ranges (not volcanoes), eastern Belgian Congo.
Gab.	Gaboon and French Equatorial Africa.
Kivu	Kivu Volcanoes in western Uganda and eastern Belgian Congo.
Uele	Upper Uele River, north central Belgian Congo.
Unk.	Unknown locality.
W. Cam.	Western Cameroons, vicinity of Cross River.

	1	2	3	4	5	6	7
Museum	Cambr.	Oslo	Oslo	Oslo	Oslo	Oslo	Oslo
Locality	Unk.	Cam.	Cam.	Unk.	Gab.	Gab.	Gab.
Museum number	1	G1	G2	G3	G4	G5	G6
Sex	male	male	male	female	male	male	male ?
Approximate age	adult	adult	adult	half gr.	adult	adult	adult
Greatest length	264	281	289	211	298	281	276
Zygomatic width	159	187	159	128	177	183	178
Cranial length	174	186	182	147	202	202	172
Cranial width	104	110	99	108	108	107	107
Cranial height	105	122	107	104	114	112	108
Orbital arc using a base of 50 mm.	75	85	72	62	79	79	75
Sagittal arc using a base of 50 mm.	74	84	90	51	88	92	65
Nasion to basion	126	148	122	108	137	133	133
Gnathion to nasion	114	112	135	95	133	102	125
Basal length	183	202	194	141	193	184	197
Condylar width	30	38	35	22	30	34	35
Outside intercondylar width	133	157	131	116	143	137	146
Outside intercoronoid width	110	138	117	93	117	—	132
Height of ascending process of ramus	80	129	112	77	101	109	103
Length of ascending process of ramus	—	—	—	—	—	—	—
Greatest width across jaws posteriorly	—	—	—	—	—	—	—
Height of occiput	—	—	—	—	—	—	—
Mastoid width	—	—	—	—	—	—	—
Orbital width	—	—	—	—	—	—	—
Length of maxillary tooth row	—	94	91	66	82	80	91
Length of mandibular tooth row	—	101	101	72	93	90	92
Outside alveolar width, upper tooth row	70	78	70	63	78	71	76
Inside alveolar width, upper tooth row	37	42	37	30	44	40	38
Mandibular width outside alveoli	64	70	62	51	61	63	68
Mandibular width inside alveoli	33	40	37	22	32	33	39
Palatal length	103	120	116	82	95	110	106
Asymmetry (right)	—	—	—	—	—	—	—
(left)	—	—	—	—	—	—	—
Museum classification	—	—	—	—	—	—	—

8 Oslo Gab. G8 female semi-ad.	9 Stock. Kivu 37 male adult	10 Stock. Kivu 31 male adult	11 Stock. Kivu 164 male adult	12 Stock. Kivu 46 male adult	13 Stock. Kivu 40 male adult	14 Stock. Kivu 41 male adult	15 Stock. Kivu 45 male adult	16 Stock. Kivu 38 male adult	17 Berlin Kivu 13254 male adult	18 Stock. Kivu 39 female adult
234	300	306	304	290	300	288	286	—	276	246
150	183	181	184	182	187	177	170	170	164	148
160	198	190	184	193	191	182	189	—	179	170
103	98	105	106	101	103	105	108	—	107	99
100	120	117	112	120	116	111	111	108	110	98
62	78	69	70	75	83	72	70	69	65	69
52	98	108 ?	88	100	94	69	69	—	67	55
113	139	134	142	147	139	140	135	127 ?	128	118
103	122	127	129	109	117	125	112	120 ?	114	103
158	204	215	227	214	223	210	205	194	195	168
32	36	34	40	40	38	35	33	38	35	33
130	144	144	156	158	155	—	133	144	138	136
116	124	121	128	117	120	—	110	104	114	104
87	140	135	132	132	129	120	124	122	120	110
—	76	77	82	73	78	72	69	73	77	58
—	55	136	129	152	152	—	137	132	132	121
—	111	93	101	108	101	100	94	—	80	70
—	172	160	165	180	175	164	159	—	144	132
—	109	112	112	113	110	107	104	100	103	94
79	94	86	93	99	98	96	100	95	90	83
85	105	99	101	106	107	104	105	105	98	91
66	73	72	73	73	80	76	73	72	70	66
36	34	37	38	36	40	38	34	32	35	39
58	67	65	68	71	74	71	70	71	65	62
32	33	35	36	38	42	38	37	36	36	30
90	129	129	139	130	136	115	125	116	121	102
—	194	204	212	198	204	200	190	190	181	163
—	202	203	212	202	207	—	192	185	186	159
—	beringei	beringei	beringei	beringei	beringei	beringei	beringei	beringei	beringei type	—

Museum Locality Museum number Sex Approximate age	19 Stock. Kivu 28 female adult	20 Stock. Kivu 42 female adult	21 Stock. Kivu 167 female adult	22 Stock. Kivu 165 male subad.	23 Berlin E. Mt. 31619 male adult	24 Stock. E. Mt. ? male adult	25 Stock. Cam. A male adult
Greatest length	257	253	—	256	302	302	273
Zygomatic width	—	145	—	167	180	177	178
Cranial length	160	172	163	171	187	181	177
Cranial width	95	98	103	114	104	97	103
Cranial height	98	98	104	112	114	120	107
Orbital arc using a base of 50 mm.	67	67	63	64	73	73	72
Sagittal arc using a base of 50 mm.	58	53	52	52	95	114	80
Nasion to basion	119	114	112	133	134	139	148
Gnathion to nasion	120	103	—	99	127	135	123
Basal length	186	171	—	192	203	210	216
Condylar width	33	35	34	36	33	35	37
Outside intercondylar width	—	130	130	151	141	148	139
Outside intercoronoid width	—	97	98	114	117	115	—
Height of ascending process of ramus	115	107	100	114	130	123	—
Length of ascending process of ramus	67	60	63	66	80	77	70
Greatest width across jaws posteriorly	—	125	117	126	133	136	120
Height of occiput	68	70	59	68	112	108	85
Mastoid width	136	142	135	149	153	151	168
Orbital width	—	97	93	102	111	113	112
Length of maxillary tooth row	83	84	—	87	94	92	81 ?
Length of mandibular tooth row	91	94	86	96	103	106 R. 103 L	90
Outside alveolar width, upper tooth row	67	69	—	63	77	77	68
Inside alveolar width, upper tooth row	38	36	—	30	40	42	38
Mandibular width outside alveoli	63	67	64	63	70	68	64
Mandibular width inside alveoli	31	35	35	33	38	38	35
Palatal length	107	107	—	114	128	131	117
Asymmetry (right)	—	168	169	177	199	209	182
(left)	—	164	166	177	201	212	182
Museum classification	—	—	mikenensis	—	graueri,type	graueri	graueri

26 Stock. Cam. B male adult	27 Stock. Cam. C male adult	28 Berlin W. Cam. 12789 male adult	29 Berlin W. Cam. 12790 male adult	30 Berlin W. Cam. A. 6309 male adult	31 Berlin W. Cam. 18515 male adult	32 Berlin Cam. 31806 female adult	33 Berlin Cam. 11652 male adult	34 Berlin Cam. 30941 male adult	35 Berlin Cam. 17960 male adult	36 Berlin W. Cam. 17963 male adult
312	272	295	279	297	290	225	284	288	327	280
176	176	183	182	—	177	154	168	171	191	166
197	165	200	186	187	185	148	178	189	220	177
111	96	101	106	97	103	98	101	97	94	109
118	105	—	113	116	115	106	112	121	123	115
75	79	81	75	70	72	65	75	77	87	65
91	87	91	71	86	83	58	96	124	150	80
141 ?	123	—	138	143	136	112	127	138	152	129
142	124	113	117	128	114	99	118	115	123	116
205 ?	182	—	199	208	196	151	188	196	217	188
40	—	34	34	36	37	34	37	33	41	37
148	—	142	142	—	140	137	—	140	163	140
124	—	121	—	122	120	115	—	118	126	123
135	—	120	126	113	106	95	125	118	124	118
82	—	79	72	76	72	64	74	74	82	71
115	—	137	125	123	130	105	—	119	151	117
98	—	—	—	—	101	74	99	94	116	—
160	168	165	174	168	158	133	151	162	170	148
102	107	119	114	110	107	96	103	113	122	115
85	81	82 ?	78 ?	85 ?	88	76	86	88	90	88
90	—	—	—	86 ?	97	83	—	94	99	95
71	66	69	71	71	70	68	70	67	81	71
42	36	40	39	40	40	40	37	37	47	39
65	—	62	63	65	62	59	65	63	73	66
34	—	34	35	37	34	30	37	34	41	36
112	109	120	115	114	109	92	111	115	112 ?	113
200	—	190	190	197	191	162.5	—	181	204	187
200	—	190	186	—	185	162.5	188	180	207	186
matschiei	graueri	diehli, type	diehli	diehli	diehli	matschiei	matschiei	matschiei	hansmeyeri type	hansmeyeri type

	37	38	39	40	41	42	43
Museum	Berlin	Berlin	Berlin	Berlin	Berlin	Berlin	Berlin
Locality	W. Cam.	W. Cam.	Gab.	Gab.	Cam.	Cam.	Cam.
Museum number	A11609 II	17658	33490	A3683	A3909	17802	30261
Sex	male	male	male	male	male	male	male
Approximate age	adult	adult	adult	adult	adult	adult	adult
Greatest length	282	316	297	294	320	305	297
Zygomatic width	177	199	172	177	187	179	179
Cranial length	162	219	196	202	212	200	192
Cranial width	102	105	98	101	104	110	102
Cranial height	108	129	115	110	—	118	100
Orbital arc using a base of 50 mm.	69	76	75	73	75	72	66
Sagittal arc using a base of 50 mm.	76	116	115	91	122	115	87
Nasion to basion	130	148	130	130	—	134	129
Gnathion to nasion	121	132	133	119	133	126	141
Basal length	188	202	182	187	—	195	187
Condylar width	42	42	36	43	39	35	37
Outside intercondylar width	152	161	139	116	151	134	145
Outside intercoronoid width	123	145	129	129	131	123	124
Height of ascending process of ramus	129	129	126	127	121	110	123
Length of ascending process of ramus	73	80	65	78	85	69	69
Greatest width across jaws posteriorly	127	132	129	114	124	110	127
Height of occiput	91	103	108	89	—	105	87
Mastoid width	159	178	157	156	172	161	154
Orbital width	110	120	111	109	116	115	108
Length of maxillary tooth row	92	93	89	92	84	87	91
Length of mandibular tooth row	103	96	88	98	92 ?	96	97
Outside alveolar width, upper tooth row	71	82	74	70	72	67	78
Inside alveolar width, upper tooth row	39	48	43	37	44	37	47
Mandibular width outside alveoli	64	68	67	65	67	62	70
Mandibular width inside alveoli	34	39	38	35	41	32	40
Palatal length	110	117 ?	115	110	121	113	111
Asymmetry (right)	181	199	178	185	204	187	183
(left)	185	198	176	184	203	187	184
Museum classification	hansmeyeri	hansmeyeri	gorilla	gorilla	jacobi	jacobi	zenkeri

44 Berlin Cam. 73 male adult	45 Berlin E. Mt. 31626 female adult	46 Berlin E. Mt. 31622 male adult	47 Berlin Kivu 13254 male adult	48 Hamb. Gab. 27 female semi-ad.	49 Hamb. Cam. 41394 male adult	50 Hamb. Unk. 40604 female adult	51 Hamb. Gab. 21 male adult	52 Hamb. Gab. 15 female adult	53 Hamb. Gab. 2a17 male subad.	54 Hamb. Gab. 2a8 female adult
291	241	287	305	234	280	235	281	267	288	250
183	148	167	172	145	185	149	171	158	163	152
207	160	180	207	150	184	166	178	172	196	169
110	90	92	96	102	109	106	101	94	102	101
120	100	109	117	—	118	99	111	101	102	111
74	60	—	73	70	69	65	74	75	75	65
103	59	—	119	52	92	51	107	94	115	57
144	116	130	143	—	135	115	142 ?	121 ?	126	124
111	110	127	129	107	123	96	121	116	126	110
190	168	197	194	—	188	157	193 ?	171 ?	179	170
34	30	—	36	31	39	31	38	32	—	—
149	125	—	144	132	145	—	148	134	—	—
126	105	—	120	101	136	—	120 ?	111	—	—
110	98	—	127	98	121	91	114	113	—	—
69	61	—	84	64	72	56	72	72	—	—
116	112	—	120	107	136	—	135	111	—	—
93	67	75	100	—	—	—	97	90	94	69
160	131	142	147	134	174	143	152	136	145	136
110	93	98	105	94	111	102	110	96	97	96
88	82	87	86 ?	—	83	77	85	84	87	85
94	87	—	—	—	95	85	93	90	—	—
72	67	73 ?	74	65	76	69	69	66	70	63
42	36	34 ?	43	33	43	40	37	35	37	31
64	63	—	64	62	67	—	64	61	—	—
35	33	—	36	35	39	—	37	33	—	—
108	103	120	113	95	105	91	100	102	106	98
186	167	—	202	163	181	—	183	171	129	121
184	168	—	202	164	178	—	180	170	132	117
zenkeri	graueri	graueri	beringei	gorilla	gorilla	gorilla	gorilla	gorilla	gorilla	gorilla

Museum Locality Museum number Sex Approximate age	55 Amst. Cam. 1911.1 male adult	56 Amst. Gab. 1912.118 male adult	57 Amst. Gab. 1904.16 male adult	58 Amst. Gab. 1912.115 male subad.	59 Amst. Gab. 1917.2 male adult	60 Amst. Cam. 1911.12 male adult	61 Amst. Cam. 1911.138 male adult
Greatest length	303	315	292	297	307 ?	296	302
Zygomatic width	180	184	161	177	182	180	182
Cranial length	187	213	199	184	207	186	194
Cranial width	100	109	99	107	107	112	106
Cranial height	124	128	107	115	113	113	115
Orbital arc using a base of 50 mm.	70	74	89	67	82	68	67
Sagittal arc using a base of 50 mm.	108	140	100	80	115	110	100
Nasion to basion	147	145	137	138	134	128	132
Gnathion to nasion	128	123	128	141	125	122	128
Basal length	214	196	187	202	192	198	199
Condylar width	34	40	33	34	37	33	38
Outside intercondylar width	142	151	136	148	135	139	156
Outside intercoronoid width	127	123	118	124	122	111	125
Height of ascending process of ramus	120	137	112	118	117	123	134
Length of ascending process of ramus	76	79	74	73	73	71	77
Greatest width across jaws posteriorly	120	125	102	126	131	132	127
Height of occiput	104	117	94	82	91	98	90
Mastoid width	159	158	195	161	160	159	175
Orbital width	106	114	106	114	111	105	113
Length of maxillary tooth row	91	83	84	93	85	90	93
Length of mandibular tooth row	100	98	88	99	95	99	97
Outside alveolar width, upper tooth row	75	71	64	76	70	74	74
Inside alveolar width, upper tooth row	42	43	32	41	36	41	43
Mandibular width outside alveoli	66	66	59	71	63	65	67
Mandibular width inside alveoli	37	36	29	40	34	38	36
Palatal length	120	110	101	119	118	110	121
Asymmetry (right)	204	207	180	193	190	134	193
(left)	202	207	180	193	191	—	193
Museum classification	gorilla	gorilla	gorilla	gorilla	gorilla	gorilla	gorilla

62 Amst. Unk. 1927.17 male adult	63 Amst. Unk. 1919.48 male adult	64 Amst. Cam. 1914.1 male adult	65 Amst. Gab. 1912.52 male subad.	66 Amst. Gab. 1908.54 male adult	67 Amst. Gab. 1891.7 male adult	68 Amst. Gab. 1921.10 male adult	69 Amst. Gab. 1912.116 male adult	70 Amst. Gab. 1919.47 male adult	71 Amst. Gab. 1912.117 male adult	72 Leiden Gab. A male adult
306	291	260	263	286	285	310	294	293	299	292
172	177	176	166	173	168	187	176	180	177	164
215	198	163	167	142	191	212	200	196	204	196
103	108	104	107	105	105	105	104	108	185	101
120	116	107	112	112	101	118	105	115	122	112
75	90	75	66	78	89	87	91	87	76	82
137	117	53	57	116	105	130	106	92	93	92
138	136	135	122	133	127	138	140	137	138	136
110	116	109	122	118	126	120	124	111	126	118
196	197	196	182	187	177	190	195	196	192	196
35	34	33	35	38	33	36	33	36	32	34
141	140	138	136	137	139	154	136	142	142	133
122	128	112	119	120	113	130	124	123	122	109
123	111	110	123	111	116	121	109	136	119	112
77	71	67	70	74	74	73	75	77	69	80
131	113	131	107	116	109	145	109	106	122	113
110	106	82	81	93	96	116	95	85	107	90
149	157	112	145	144	149	165	170	154	157	158
107	111	116	104	109	101	115	126	113	107	112
91	92	94	89	81	82	90	82	88	87	84
99	100	102	94	86	86	110	87	95	96	88
77	73	73	72	66 ?	67	80	71	71	73	70
44	41	41	42	39 ?	34	47	40	39	43	—
69	65	67	64	59	57	70	63	67	65	63
39	35	38	37	35	31	41	37	36	37	—
123	119	115	107	110	106	121	111	112	110	107
194	185	189	178	184	185	204	189	192	188	179
194	185	185	184	183	182	205	188	196	190	176
gorilla	gorilla	—	—	gorilla	—	—	gorilla	gorilla	gorilla	gorilla

Museum Locality Museum number Sex Approximate age	73 Leiden Gab. 2 female subad.	74 Leiden Gab. Cat. C. male adult	75 Leiden Gab. B. male subad.	76 Tervueren Cam. R.G. 5585 male adult	77 Tervueren Cam. R.G. 63 male subad.	78 Tervueren E. Mt. R.G. 8187 male adult	79 Tervueren E. Mt. R.G. 9220 male adult
Greatest length	229	285	253	304	381	304	310
Zygomatic width	151	180	156	185	164	182	176
Cranial length	161	199	173	201	191	193	200
Cranial width	110	101	102	103	100	101	96 ?
Cranial height	99	114	104	120	112	116	113
Orbital arc using a base of 50 mm.	67	78	74	80	77	70	68
Sagittal arc using a base of 50 mm.	52	89	55	128	85	107	—
Nasion to basion	111	133	124	141	133	136	133
Gnathion to nasion	100	117	116	129	112	121	125
Basal length	158	180	170	202	190	207	194
Condylar width	29	—	—	44	29	31	43
Outside intercondylar width	127	—	—	151	129	135	153
Outside intercoronoid width	114	—	—	126	112 ?	120	121
Height of ascending process of ramus	99	—	—	127	112	144	141
Length of ascending process of ramus	60	—	—	78	66	79	80
Greatest width across jaws posteriorly	94	—	—	142	101	160	133
Height of occiput	63	100	63	107	77	105	105
Mastoid width	137	166	140	166	143	171	153
Orbital width	99	101	95	109	110	110	107
Length of maxillary tooth row	75	87	85	94	34	106	86
Length of mandibular tooth row	82	—	—	104	90	115	95
Outside alveolar width, upper tooth row	66	75	62	74	68	78	74
Inside alveolar width, upper tooth row	38	41	33	40	37	33	38
Mandibular width outside alveoli	58	—	—	66	64	71	65
Mandibular width inside alveoli	33	—	—	35	36	34	36
Palatal length	92	105	96	121	107	134	129
Asymmetry (right)	156	125	117	197	184	195	199
(left)	154	128	118	198	182	203	200
Museum classification	gorilla	gorilla	gorilla	matschiei	mayema	—	—

80 Tervueren E. Mt. 999 male subad.	81 Tervueren E. Mt. 994 male adult	82 Tervueren E. Mt. 1001 male adult	83 Tervueren E. Mt. 998 male subad.	84 Tervueren Kivu 2257 male adult	85 Tervueren Gab. 9291 male adult	86 Tervueren Gab. 9006 male subad.	87 Tervueren Uele 100 male adult	88 Tervueren Uele 101 female subad.	89 Tervueren Uele 102 female adult	90 Tervueren E. Mt. 103 male adult
310	296	291	284	343	316	356	309	240	216	—
175	168	181	170	180	179	154	181	162	147	—
195	188	188	177	215	205	173	213	156	145	—
97	94	102	103	105	103	101	94	106	100	—
115	116	113	110	122	118	98	110	112	97	—
63	72	70	73	73	82	68	85	64	62	—
75	94	93	72	118	124	55	129	53	55	—
138	142	135	132	147	145	131	127 ?	126	107	—
133	123	125	128	140	129	115	127	106	97	—
206	206	207	197	227	213	181	183 ?	173	150	—
33	37	36	33	34	40	30	—	—	31	35
143	144	141	137	160	149	143	—	—	120	143
115	111	121	113	134	128	117	—	—	109	124
124	118	131	120	150	122	106	—	—	98	126
79	75	81	75	79	81	93	—	—	59	67
129	130	140	135	156	120	116	—	—	95	125
84	95	89	97	131	100	64	—	66	—	—
156	143	152	153	158	158	143	154	147	122	—
102	104	108	107	109	117	104	111	106	90	—
106	97	93	91	93	92	80	78	80	74	—
100	100	101	102	103	99	96	—	—	83	—
76	74	76	72	73	73	70	77	67	62	—
40	39	40	39	39	38	37	47	38	32	—
70	69	69	66	70	67	62	—	—	56	67
37	38	38	36	38	35	32	—	—	29	37
124	123	130	123	138	124	94	109	104	88	—
204	197	200	197	203	205	175	—	—	157	192
203	200	202	197	201	201	177	—	—	156	192
graueri	graueri	graueri	graueri	beringei	gorilla	gorilla	uellensis	uellensis	uellensis	uellensis

Museum Locality Museum number Sex Approximate age	91 Tervueren E. Mt. 804 male adult	92 Tervueren E. Mt. 9405 male adult	93 Tervueren Kivu 3360 male adult	94 Tervueren Kivu 8607 female adult	95 Tervueren Kivu 3608 male subad.	96 Tervueren Kivu 2263 female adult	97 Tervueren Kivu 1002 male young
Greatest length	309	320	330	232	262	247	248
Zygomatic width	174	182	190	146	153	148	152
Cranial length	191	188	218	165	169	172	162
Cranial width	97	104	105	98	101	104	102
Cranial height	115	118	115	97	101	103	106
Orbital arc using a base of 50 mm.	67	72	80	80	68	67	60
Sagittal arc using a base of 50 mm.	120	113	109	62	56	54	54
Nasion to basion	143	143	144	119	129	120	120
Gnathion to nasion	135	149	133	93	105	104	104
Basal length	212	222	220	169	199	172	172
Condylar width	33	40	44	36	36	36	29
Outside intercondylar width	145	149	168	128	137	135	129
Outside intercoronoid width	117	122	124	114	100	109	104
Height of ascending process of ramus	126	120	133	111	108	104	103
Length of ascending process of ramus	81	80	87	62	61	58	63
Greatest width across jaws posteriorly	136	135	148	126	125	115	115
Height of occiput	107	112	—	72	68	68	68
Mastoid width	154	164	165	135	151	134	141
Orbital width	106	104	110	99	93	96	95
Length of maxillary tooth row	95	94	102	85	93	84	83
Length of mandibular tooth row	103	110	112	88	98	88	(80)
Outside alveolar width, upper tooth row	79	76	77	72	72	65	71
Inside alveolar width, upper tooth row	42	41	37	35	37	29	37
Mandibular width outside alveoli	72	69	74	66	63	63	69
Mandibular width inside alveoli	38	37	39	36	35	33	36
Palatal length	127	139	137	107	118	100	104
Asymmetry (right)	204	212	211	156	181	159	171
(left)	208	207	218	162	178	164	171
Museum classification	graueri	graueri	beringei	beringei	beringei	beringei	beringei

98 Tervueren E. Mt. 1700 male adult	99 Tervueren E. Mt. 806 female adult	100 Paris Gab. ? male subad.	101 Paris Gab. An. 286 male adult	102 Paris Gab. An. 1912.475 male semi-ad.	103 Paris Gab. — male adult	104 Paris E. Mt. 1921.133 male adult	105 Anat. P. Gab. 1900.502 male adult	106 Anat. P. Gab. ? male adult	107 Anat. P. Gab. A. 16664 male adult	108 Anat. P. Gab. A. 10663 male adult
300	237	281	313	291	331	310	280	202	320	300
182	150	181	176	173	191	180	169	169	180	177
181	153	182	216	185	226	183	195	194	220	212
97	97	108	96	103	102	103	104	100	101	103
116	103	107	115	109	128	115	108	122	112	105
69	64	75	77	76	94	68	79	77	65	75
97	57	90	110	61	107	107	109	90	135	95
135	121	127	136	140	158	135	133	140	138	131
144	106	116	114	130	121	141	129	101	128	121
204	174	189	193	207	223	218	189	193	194	180
34	30	42	35	33	42	42	29	37	35	35
146	128	158	146	136	158	142	128	145	147	144
119	104	128	123	117	131	116	111	121	137	118
129	101	117	130	111	138	123	105	121	114	115
79	64	73	77	82	81	80	64	73	71	93
144	109	137	131	103	109	129	98	123	133	113
92	67	—	105	84	113	93	80	95	112	97
154	131	166	166	152	175	142	145	164	173	147
108	95	113	115	104	128	107	104	105	118	108
100	80	90	84	90	94	95	94	79	88	86
107	88	96	91	100	99	106	90	87	98	91
79	70	71	73	71	79	76	71	65	71	67
41	38	41	41	39	46	41	39	37	40	35
72	66	65	66	59	69	70	63	60	66	58
40	38	36	38	28	40	38	37	34	36	31
128	102	107	111	126	120	132	105	113	111	104
210	165	187	185	202	207	207	130	178	193	183
210	166	185	185	203	205	207	131	182	195	184
graueri	graueri	—	—	—	—	—	—	—	—	—

Museum Locality Museum number Sex Approximate age	109 Brit. M. Gab. 23.11.29.4 male adult	110 Brit. M. Gab. 25.1.4.1 male adult	111 Brit. M. Gab. 23.11.29.7 male adult	112 Brit. M. Gab. 23.11.29.1 male adult	113 Brit. M. Gab. 23.11.29.3 male adult	114 Brit. M. Gab. 25.1.4.3 male adult	115 Brit. M. Gab. 23.11.29.2 male adult
Greatest length	283	290	296	293	308	274	262
Zygomatic width	167	177	180	179	172	169	165
Cranial length	184	168	192	194	185	168	162
Cranial width	99	101	107	104	97	107	100
Cranial height	109	119	115	105 ?	105 ?	105	102
Orbital arc using a base of 50 mm.	76	79	70	86	70	72	66
Sagittal arc using a base of 50 mm.	90	121	103	78	116	80	90
Nasion to basion	127	146	135	129 ?	124 ?	126	125
Gnathion to nasion	116	127	124	129	145	116	117
Basal length	186	211	186	184 ?	195 ?	187	182
Condylar width	37	37	35	38	32	35	32
Outside intercondylar width	135	138	140	156	135	148	132
Outside intercoronoid width	112	120	126	120	121	124	117
Height of ascending process of ramus	122	116	124	120	112	115	109
Length of ascending process of ramus	71	80	70	79	71	68	73
Greatest width across jaws posteriorly	107	113	127	124	113	117	108
Height of occiput	—	111	108	—	—	92	—
Mastoid width	153	157	165	166	163	161	144
Orbital width	110	104	109	113	105	104	105
Length of maxillary tooth row	88	89	91	90	92	99	78
Length of mandibular tooth row	91	107	94	99	96	102	86
Outside alveolar width, upper tooth row	75	75	75	74	72	67	70
Inside alveolar width, upper tooth row	42	45	43	40	37	33	38
Mandibular width outside alveoli	67	67	65	64	64	63	62
Mandibular width inside alveoli	38	39	34	44	33	31	36
Palatal length	110	123	111	117	100	114	102
Asymmetry (right)	178	198	180	194	187	190	185
(left)	175	197	180	195	187	185	186
Museum classification	gorilla	gorilla	gorilla	gorilla	gorilla	gorilla	gorilla

116 Brit. M. Kivu 22.2.10.1 male adult	117 Brit. M. Gab. 25.1.4.2 male adult	118 Dayrell W. Cam. 7.1.8.1 male subad.	119 Dayrell W. Cam. 13.2.2.2 male adult	120 Dayrell W. Cam. 13.2.2.1 male adult	121 Brit. M. Kivu 20.4.13.4 male subad.	122 Brit. M. Unk. 1011.A. male adult	123 Brit. M. E. Mt. 1927 male adult	124 R. C. S. Cam. Ca. 22.4.20 male adult	125 R. C. S. Kivu 22.2.Ca. G.10 male adult	126 R. C. S. Gab. 21.A. Ca.570 male adult
302	298	260	275	278	267	299	293	314	289	299
182	174	172	172	185	165	167	188	183	171	177
190	189	161	175	180	175	190	180	198	193	198
103	104	97	99	94	97	100	98	106	105	103
116	114	—	—	110	106	108	118	125	114	106
69	75	77	74	68	71	81	67	69	83	81
120	83	76	115	103	77	110	102	108	120	113
143 ?	145	—	—	134	127	135	143	146	133	128
128	130	119	116	115	104	131	129	126	115	115
216	203	—	—	193	179	190	214	223	189	183
42	38	—	—	—	—	34	38	43	34	35
162	147	—	—	—	—	142	147	162	141	139
119	119	—	—	—	—	113	118	122	123	127
124	104	—	—	—	—	118	131	132	118	115
79	76	—	—	—	—	75	88	88	74	73
137	119	—	—	—	—	117	149	143	122	110
106	—	—	—	91	91	97	91	115	89	111
165	169	152	154 ?	158	164	144	164	158	161	157
102	112	102	103	104	102 ?	102	111	111	108	111
93	87	79	79	87	83 ?	84	93	95	84	89
101	95	68	68 ?	71	—	89	103	104	90	89
74	74	40	34 ?	40	70	67	74	73	73	69
37	43	—	—	—	37	38	40	37	42	39
68	66	—	—	—	—	58	69	66	64	65
34	36	—	—	—	—	31	38	35	36	36
115 ?	116	105	96	114	109	107	132	135	107	105
198	195	118	117	129	114	181	202	208	187	189
201	193	116	120	125	113	180	203	209	185	184
beringei	—	diehli	diehli	diehli	beringei	gorilla	graueri	—	—	—

Museum Locality Museum number Sex Approximate age	127 R. C. S. Gab. 21 male adult	128 R. C. S. Unk. 22 male adult	129 R. C. S. W. Cam. 25.5 male adult	130 R. C. S. W. Cam. Ca. 570.22.3 male adult	131 R. C. S. W. Cam. 23.28 male adult	132 R. C. S. W. Cam. 23.25 male adult	133 R. C. S. W. Cam. 23.23 male adult
Greatest length	305	292	284	282	279	300	276
Zygomatic width	177	170	178	174	181	—	170
Cranial length	198	195	193	173	181	198	182
Cranial width	104	92	95	102	103	94	100
Cranial height	112	97 ?	109 ?	108 ?	113	—	107 ?
Orbital arc using a base of 50 mm.	72	81	80	72	74	73	69
Sagittal arc using a base of 50 mm.	99	135	100	83	90	107	85
Nasion to basion	135	120 ?	132 ?	134 ?	144	—	123 ?
Gnathion to nasion	131	122	117	118	117	123	113
Basal length	193	170 ?	183 ?	202 ?	201	—	168 ?
Condylar width	32	—	—	—	—	—	—
Outside intercondylar width	145	—	—	—	—	—	—
Outside intercoronoid width	125	—	—	—	—	—	—
Height of ascending process of ramus	124	—	—	—	—	—	—
Length of ascending process of ramus	72	73	—	—	—	—	—
Greatest width across jaws posteriorly	119	—	—	—	—	—	—
Height of occiput	97	—	—	—	—	—	—
Mastoid width	152	152	152	164	167	169	164
Orbital width	105	104	107	111	112	110	108
Length of maxillary tooth row	91	81	81	81	89	90	79
Length of mandibular tooth row	96	89	—	—	—	—	—
Outside alveolar width, upper tooth row	75	72	74	69	70	71	71
Inside alveolar width, upper tooth row	43	44	43	41	41	40	42
Mandibular width outside alveoli	65	63	—	—	—	—	—
Mandibular width inside alveoli	39	35	—	—	—	—	—
Palatal length	110	104	102	111 ?	107	104	109
Asymmetry (right)	189	121	131	120	131	127	118
(left)	188	123	127	121	133	129	121
Museum classification	—	—	—	diehli ?	diehli ?	diehli ?	diehli ?

134 R. C. S. W. Cam. 23.27 male adult	135 R. C. S. W. Cam. 23.26 male adult	136 R. C. S. W. Cam. 23.22 male adult ?	137 R. C. S. W. Cam. 23.24 male subad.	138 R. C. S. W. Cam. 23.29 male adult	139 Tring Gab. — male adult	140 Tring Cam. ad. 15 male adult	141 Tring Kivu ad. 33 male adult	142 Tring Gab. ad. 16 male adult	143 Tring Gab. ad. 41 male adult	144 Tring Gab. ad. 44 male adult
288	290	278	283	294	344	314	304	295	303	306
172	170	169	172	167	200	187	182	180	172	164
194	173	198	175	198	228	207	201	188	208	210
101	100	101	105	94	103	102	103	105	106	99
106 ?	115	116	96 ?	120	132	117	115	122	105	116
80	70	77	70	81	91	77	77	69	79	86
98	102	110	79	116	185	152	98	98	127	132
121 ?	138	139	118 ?	136	152	134	141	151	131	141
119	134	104	128	117	134	139	117	121	125	117
182 ?	204	186	186 ?	194	222	197	210	214	182	193
—	—	—	—	—	48	43	37	37	32	35
—	—	—	—	—	166	167	150	150	138	137
—	—	—	—	—	136	143	125	129	117	108
—	—	—	—	—	152	135	123	133	111	112
—	—	—	—	—	89	78	76	80	74	76
—	—	—	—	—	131	131	135	134	101	116
—	—	—	—	—	139	106	112	99	100	104
—	155	162	151	167	175	170	167	164	143	142
106	107	111	109	108	124	114	113	114	106	110
84	85	89	80	79 ?	96	88	100	92	80	83
—	—	—	—	—	104	100	109	99	87	89
69	71	76	63	64 ?	83	74	75	82	72	67
38	44	43	36	34 ?	49	43	39	47	41	37
—	—	—	—	—	76	73	71	73	63	60
—	—	—	—	—	44	44	38	41	36	34
108	112	104	112	113	129	130 ?	131	129	106	107
128	139	116	132	132	223	200	197	209	187	184
131	136	118	134 ?	132	224	196	204	210	186	184
diehli ?	diehli ?	diehli ?	diehli ?	diehli ?	diehli ?	matschiei	kivu gor.	matschiei	—	—

Museum Locality Museum number Sex Approximate age	145 Tring Gab. ad. 23 male adult	146 Tring Gab. ad. 34 male adult	147 Tring Gab. ad. 14 male adult	148 Tring Gab. ad. 45 male adult	149 Tring Gab. ad. 31 male adult	150 Tring W. Cam. A. 40 male subad.	151 Tring W. Cam. A. 34 male adult
Greatest length	271	290	315	305	314	283	265
Zygomatic width	181	168	176	—	175	185	170
Cranial length	188	207	219	190	205	193	180
Cranial width	99	100	100	100	99	109	90
Cranial height	112	110	114	108	104	103	89 ?
Orbital arc using a base of 50 mm.	81	80	91	74	78	69	77
Sagittal arc using a base of 50 mm.	98	97	130	115	117	104	107
Nasion to basion	128	134	142	140	137	132	114 ?
Gnathion to nasion	108	121	116	129	131	109	119
Basal length	175	183	206	207	197	185	179 ?
Condylar width	31	33	39	33	42	—	—
Outside intercondylar width	130	144	147	141	146	—	—
Outside intercoronoid width	114	122	131	121	123	—	—
Height of ascending process of ramus	115	117	138	124	129	—	—
Length of ascending process of ramus	75	72	82	75	73	—	—
Greatest width across jaws posteriorly	106	108	135	132	138	—	—
Height of occiput	110	88	113	99	97	—	—
Mastoid width	145	153	168	170	166	154	154
Orbital width	106	115	117	103 ?	112	108	107
Length of maxillary tooth row	87	85	89	91	96	82	82
Length of mandibular tooth row	95	92	101	98	100	—	—
Outside alveolar width, upper tooth row	66	73	72	74	73	67	69 ?
Inside alveolar width, upper tooth row	33	37	40	42	39	37	38 ?
Mandibular width outside alveoli	60	64	65	69	66	—	—
Mandibular width inside alveoli	31	34	35	39	33	—	—
Palatal length	98	102	123	113	112	97	102
Asymmetry (right)	173	186	203	197	195	120	129
(left)	171	182	203	199	193	118	128
Museum classification	—	—	—	—	—	—	diehli ?

152 Tring Cam. A. 43 male adult	153 Tring Cam. A. 39 male adult	154 Tring Gab. A. 19 male adult	155 Tring Gab. A. 21 male adult	156 Tring Cam. A. 32 male adult	157 Tring Cam. A. 24 male adult	158 Tring Unk. A. 22 male adult	159 Tring Unk. A. 29 male adult	160 Tring Unk. A. 27 male adult	161 Tring Unk. A.20 male adult	162 Tring Unk. A. 17 male adult
297	317	295	278	307	278	272	283	296	269	272
180	167	166	173	187	174	179	172	177	172	166
192	209	204	180	208	183	185	191	190	170	174
102	94	96	102	101	106	105	98	102	99	96
106 ?	106 ?	109	106	115 ?	95 ?	—	98 ?	110	113	111
79	76	71	72	83	69	76	81	63	76	68
122	140	125	117	138	93	74	132	103	105	135
128 ?	127 ?	130	124	140 ?	101 ?	—	124 ?	135	136	127
130	134	121	121	120	111	115	121	125	111	112
191 ?	192 ?	184	182	192 ?	160 ?	—	168 ?	201	185	182
—	—	32	29	36	34	34 L. 36 R.	33	36 L. 39 R.	32 L. 33 R.	34
—	—	137	135	150	144	158	138	144	135	136
—	—	115	114	128	126	137	120	124	115	112
—	—	125	113	125	118	127	125	126	105	119
—	—	71	71	81	72	75	73	77	72	69
—	—	115	117	138	124	113	115	118	119	124
—	—	96	88	—	—	—	—	96	99	91
155	153	145	157	163	155 ?	165	155	161	143	144
110	102	106	105	123	112	111	109	119	103	102
82 ?	75 ?	90	87	93	81	87	87	84	84	90
—	—	92	91	101 ?	92	94	93	91	87	95
71	71 ?	69	67	72	68	72	73	75	70	68
41	40	37	35	35	37	42	39	44	40	37
—	—	62	61	68	62	71 ?	71 M_3	65	62	61
—	—	33	31	34	33	39 ?	37 M_3	35	36	31
109	110	109	105	114	103	118	108	112	103	95
135	128	179	182	193	177	187	176	196	181	181
129	128	178	181	194	175	186	181	194	179	180
—	—	—	—	—	—	—	—	—	—	—

Museum Locality Museum number Sex Approximate age	163 Tring Unk. A. 36 ? adult	164 Tring Unk. A. 30 ? male adult	165 Tring Gab. 3 male adult	166 Tring Unk. ? male adult	167 Quex Gab. 195 male adult	168 Quex Gab. 163 male adult	169 Quex Gab. 162 male adult
Greatest length	275	273	288	314	304	312	333
Zygomatic width	161	149	174	196	184	174	180
Cranial length	184	187	186	204	201	201	232
Cranial width	103	97	102	110	110	107	105
Cranial height	99	112	—	120	106	105	122
Orbital arc using a base of 50 mm.	72	81	74	74	70	55	85
Sagittal arc using a base of 50 mm.	91	109	67	155	85	102	134
Nasion to basion	124	127	—	134	127 ?	129	146
Gnathion to nasion	126	112	116	139	114	132	139
Basal length	174	174	—	194	191 ?	195	191
Condylar width	32	34	—	44	41	34	37
Outside intercondylar width	137	130	—	169	151	153	154
Outside intercoronoid width	114	115	—	136	136	127	123
Height of ascending process of ramus	108	96	—	111	137	119	130
Length of ascending process of ramus	67	66	—	80	75	80	78
Greatest width across jaws posteriorly	114	103	—	134	128	128	138
Height of occiput	87	93	—	106	—	—	—
Mastoid width	140	135	170	171	177	158	177
Orbital width	104	96	115	115	121	108	115
Length of maxillary tooth row	82	87	87	90	88	88	87
Length of mandibular tooth row	86	89	—	101	94	87	97
Outside alveolar width, upper tooth row	70	66	70	74	72	71	73
Inside alveolar width, upper tooth row	39	34	39	41	42	38	44
Mandibular width outside alveoli	64	59	—	74	63	63	67
Mandibular width inside alveoli	36	31	—	43	37	33	36
Palatal length	103	104	108	123	118	127	113
Asymmetry (right)	173	169	123	204	199	200	199
(left)	175	172	118	200	198	204	197
Museum classification	—	castaneiceps	—	—	—	—	—

170 Quex Gab. 206 male subad.	171 Quex Gab. 216 male subad.	172 Quex Gab. 225 male adult	173 Quex Gab. 207 male subad.	174 Quex Gab. 196 male adult	175 Quex Gab. 159 male adult	176 M. C. Z. Gab. 9586 male adult	177 M. C. Z. Cam. 23162 male adult	178 M. C. Z. Cam. 20039 male adult	179 M. C. Z. Cam. 23160 male adult	180 M. C. Z. Cam. 20038 male adult
271	295	305	278	269	299	279	326	314	331	299
—	—	175	178	171	167	167	182	187	183	183
178	200	201	191	175	206	187	222	205	212	194
105	98	104	106	98	104	97	101	100	101	102
110	104	—	125	—	115	101	111	117	119	119
76	78	73	70	69	71	76	82	80	71	95
65	126	115	107	67	131	107	132	96	124	94
138	131	141	143	—	141	130	144	147	142	169
110	114	127	104	121	124	113	141	135	139	151
201	189	196	195	—	192	182	201	211	215	197
—	—	—	—	33	31	35	42	37	42	34
—	—	—	—	137 ?	133	131	149	150	140	145
124	—	—	—	122	118	118	124	122	126	126
—	—	—	—	109	110	113	126	125	130	118
71	—	—	—	69	70	70	80	85	81	73
126	—	—	—	127	113	129	133	124	133	119
80	—	—	88	—	96	94	103	105	114	106
154	—	161	159	147	162	155	162	163	162	171
107	109	116	119	105	105	103	114	118	112	123
95	—	—	73	92	86	85	87	89	93	97
89	—	—	—	104	88	90	97	98	100	100
70	—	—	71	74	68	67	79	75	74	76
40	—	32 ?	43	40	37	37	49	43	39	40
65	—	—	—	71	60	63	70	68	67	68
37 ?	—	—	—	39	32	32	40	38	35	36
119	110	112	105	116	109	97	115	123	127	112
—	—	133	187	187	183	178	209	205	201	199
—	—	138	186	187	181	?	206	203	207	195
—	—	—	—	—	—	—	—	—	—	—

	181	182	183	184	185	186	187
Museum	M. C. Z.	H. C.	Field	Field	A.M.N.H.	A.M.N.H.	A.M.N.H.
Locality	E. Mt.	Unk.	Kivu	E. Mt.	Gab.	Gab.	Gab.
Museum number	23182	1	26065	27551	C.A. 503	C.A. 508	C.A. 500
Sex	male	male	male	male	male	male	male
Approximate age	adult	adult	adult	adult	adult	adult	adult
Greatest length	318	325	295	304	262	267	281
Zygomatic width	180 ?	171	179	179	175	168	173
Cranial length	195	214	176	183	178	179	197
Cranial width	100	95	104	107	100	108	100
Cranial height	115	117	190	122	105	109	115
Orbital arc using a base of 50 mm.	66	74	67	71	85	71	71
Sagittal arc using a base of 50 mm.	125	125	97	114 ?	92	71	117
Nasion to basion	143	144 ?	142	142	133	130	137
Gnathion to nasion	150	143	131	137	103	106	107
Basal length	233	207 ?	214	218	184	186	183
Condylar width	34	36	39	42	35	32	35
Outside intercondylar width	—	149	160	148	141	140	142
Outside intercoronoid width	—	125	117	124	122	112	120
Height of ascending process of ramus	130	132	125	123	118	111	112
Length of ascending process of ramus	87	77	83	80	71	64	67
Greatest width across jaws posteriorly	—	136	132	132	123	133	124
Height of occiput	109	—	100	111	91	91	—
Mastoid width	152	158	169	153	161	161	152
Orbital width	106	115	115	112	115	107	112
Length of maxillary tooth row	97	86	101	93	86	80	90
Length of mandibular tooth row	112	93	108	104	97	91	99
Outside alveolar width, upper tooth row	80	75	74	77	74	70	74
Inside alveolar width, upper tooth row	40	44	34	40	41	37	39
Mandibular width outside alveoli	68	68	71	68	66	61	65
Mandibular width inside alveoli	40	37	37	37	37	33	33
Palatal length	144	130	132	126	108	105	107
Asymmetry (right)	220	197	139	138	117	120	124
(left)	—	195	137	141	115	119	128
Museum classification	—	—	—	—	—	—	—

188 A.M.N.H. Gab. C.A. 506 male adult	189 A.M.N.H. Gab. C.A. 504 male adult	190 A.M.N.H. Gab. C.A. 502 male adult	191 A.M.N.H. Gab. C.A. 501 male adult	192 A.M.N.H. Gab. C.A. 507 male adult	193 A.M.N.H. Gab. C.A. 505 male adult	194 A.M.N.H. — 54328 B male adult	195 A.M.N.H. — A. male adult	196 A.M.N.H. Cam. 54355 male adult	197 A.M.N.H. Kivu 54087 male adult	198 A.M.N.H. Gab. 69398 male adult
277	257	305	284	273	295	296	279	299	293	275
165	171	183	175	170	180	188	177	177	180	169
174	174	191	178	178	186	193	195	192	192	176
107	102	91	100	106	104	110	109	97	104	95
115	107	118	113	125	110	113	107	110	117	107
76	79	77	72	78	76	80	80	85	75	69
105	74	117	91	95	96	80	78	100	87	85
141	134	148	133	150	133	146	133	139	143	135
126	96	136	130	116	132	135	122	122	107	119
191	179	211	191	201	186	210	180	202	220	195
30	29	36	28	33	34	36	38	40	41	35
136	132	154	130	147	138	157	150	149	148	139
113	120	125	119	122	120	130	126	123	117	116
118	109	115	110	119	110	115	113	124	125	105
70	70	78	73	71	69	74	68	81	81	75
117	111	137	125	114	114	143	129	128	144	117
99	85	108	—	96	106	90	85	93	104	83
144	156	164	154	153	167	172	168	157	179	150
104	107	116	104	110	102	119	110	107	108	102
81	81	96	90	85	82	91	87	90	90	94
93	91	100	96	97	95	99	94	98	95	96
69	67	77	72	72	71	74	72	77	76	70
39	37	41	39	39	36	40	38	38	39	35
65	60	70	68	66	63	66	68	69	74	61
34	31	39	37	36	32	36	37	34	45	32
113	103	124	106	110	113	128	100	116	125	106
127	118	137	131	124	121	146	122	135	119	128
126	121	136	131	124	121	147	116	135	116	129
—	—	—	—	—	—	—	—	—	—	—

Museum Locality Museum number Sex Approximate age	199 A.M.N.H. Kivu 54090 male adult	200 U.S.N.M. Gab. 174716 male adult	201 U.S.N.M. Gab. 174712 male adult	202 U.S.N.M. Gab. 174713 male adult	203 U.S.N.M. Cam. 176224 male adult	204 U.S.N.M. Cam. 176203 male adult	205 U.S.N.M. Gab. 174715 male adult
Greatest length	305	272	283	289	300	291	302
Zygomatic width	179	163	177	163	—	188	173
Cranial length	200	182	185	195	202	191	203
Cranial width	107	100	106	94	101	107	108
Cranial height	115	104	110	107	121	126	112
Orbital arc using a base of 50 mm.	77	72	81	90	80	77	67
Sagittal arc using a base of 50 mm.	84	93	95	102	115	87	103
Nasion to basion	141	128	136	141	143	152	132
Gnathion to nasion	116	125	129	122	111	118	129
Basal length	209	174	186	191	192	204	186
Condylar width	35	33	—	34	—	43	34
Outside intercondylar width	146	133	—	—	—	155	142
Outside intercoronoid width	116	109	—	110	—	123	121
Height of ascending process of ramus	123	110	—	113	—	114	123
Length of ascending process of ramus	77	66	—	74	—	71	71
Greatest width across jaws posteriorly	142	110	—	127	—	125	122
Height of occiput	104	86	91	96	119	104	106
Mastoid width	174	140	101	148	176	175	154
Orbital width	110	107	108	104	111	118	113
Length of maxillary tooth row	95	86	81	78	86	83	83
Length of mandibular tooth row	102	95	—	90	—	99	90
Outside aveolar width, upper tooth row	74	69	73	71	73	80	73
Inside alveolar width, upper tooth row	35	37	41	41	38	41	44
Mandibular width outside alveoli	72	57	—	61	—	69	65
Mandibular width inside alveoli	40	31	—	35	—	39	38
Palatal length	129	101	107	115	115	112	106
Asymmetry (right)	122	125	132	127	132	131	132
(left)	131	128	135	129	130	132	133
Museum classification	—	—	—	—	—	—	—

206 U.S.N.M. Cam. 176215 male adult	207 U.S.N.M. Cam. 176210 male adult	208 U.S.N.M. Gab. 220325 male adult	209 U.S.N.M. Cam. 176205 male adult	210 U.S.N.M. Cam. 176209 male adult	211 U.S.N.M. Cam. 176212 male adult	212 U.S.N.M. Gab. 174719 male adult	213 U.S.N.M. Gab. 174722 male adult
270	288	278	314	285	285	282	277
186	—	163	167	182	180	172	167
194	190	185	214	197	184	189	190
107	113	104	98	108	97	108	104
113	—	116	116 ?	120	114	101	102
72	66	78	82	81	82	73	75
85	68	92	138	95	116	98	75
133	—	134	136 ?	147	140	128	131
104	130	116	134	103	122	122	121
180	—	188	197 ?	200	191	183	178
37	—	32	36	—	39	—	32
144	—	123 ?	147	—	145	—	132
132	—	102 ?	120	—	125	—	116
123	—	110	118	—	125	—	109
69	—	67	73	—	75	—	70
133	—	104 ?	111	—	123	—	107
—	77	87	—	100	97	—	80
161	173	152	147	156	169	147	147
116	115	111	110	120	118	116	109
89	87	87	88	86	81	84	86
100	—	95	98	—	95	—	88
77	72	70	77	76	—	72	70
43	40	39	44	44	—	42	37
68	—	62^{M}	67	—	67	—	61
35	—	36^{M}	34	—	35	—	32
106	111	101	125	114	105	105	105
117	120	119	138	123	132	123	133
115	141 ?	117	141	126	138	128	136
—	—	—	—	—	—	—	—

Average Skull Measurements and Curves.

As explained under "Methods," for purposes of comparison, all skull measurements have been reduced to percentages of the basal length. They are compared on the basis of averages of measurements and also from the result of a study of their curves which show percentages common to most skulls from a given region. In this study the height of the curves is of less significance, for that characteristic indicates the *number* of skulls. It is the shapes of the curves as well as the relation of the peaks that are most important. In all cases I had more Gaboon skulls than others and the Cameroons come next, with the Kivu and Eastern Mountain about even, and the Western Cameroons least.

The following abbreviations will be used: —

Average — to mean average of similar measurements for a given locality.

Curve — to mean percentages common to most skulls of a given region as shown by the maximum peak of their curve.

Gab.— Gaboon; *Cam.*— Cameroons; *W. Cam.*— Western Cameroons; *Kivu* — Volcano gorillas; *E. Mt.*— Eastern mountain ranges of the Belgian Congo.

When two numbers are given under the curve column it means they are both paaks of equal height when separated by *and*. When separated by a (—) the peak is continuous from one to the other. When two peaks are mentioned and one is a little higher than the other the maximum has an (*M*) beside it.

LENGTH MEASUREMENTS.

1. The greatest or *total length* (gnathion to inion): —

	Average		*Curve*
Gab.	152	Gab.	160
Cam.	151	Cam.	150–155
W. Cam.	150	W. Cam.	150
E. Mt.	144	E. Mt.	144
Kivu	141.5	Kivu	140

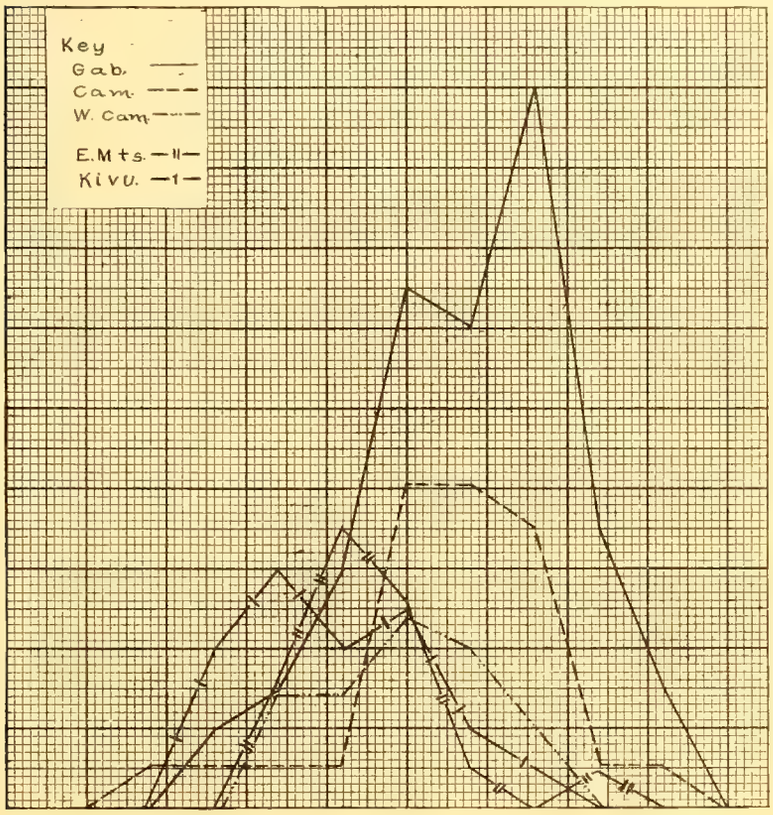

FIG. 1.— Total length.

This seems to indicate a division into two groups, the coast and the mountain.

2. *Basal length* (basion to gnathion). — In this case the exact measurements are used.

	Average		*Curve*
E. Mt.	206.5	E. Mt.	210
Kivu	201.5	Kivu	195 (M) and 210
Cam.	196.5	Cam.	195–200
Gab.	191	W. Cam.	190 and 205
W. Cam.	190.5	Gab.	185 and 195 (M)

The curve has a great many peaks. These figures give the Kivu and Eastern Mountain gorilla the greatest basal length with the Cameroons a close second. The Gaboon and Western Cameroons tend to group together with the shortest basal length.

3. *Palatal length* (gnathion to anteriormost point of hind edge of palate): —

Average		*Curve*	
E. Mt.	62	E. Mt.	64
Kivu	61	Kivu	62
Cam.	58.5	Cam.	60
Gab.	57.5	Gab.	58 (M) and 60
W. Cam.	56.5	W. Cam.	56

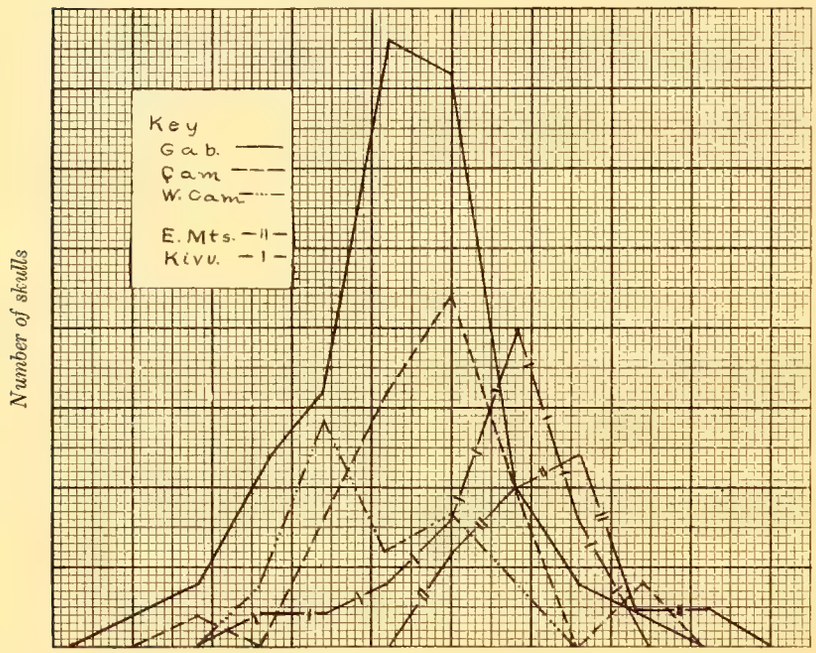

FIG. 2.— Palatal length.

The Kivu and Eastern Mountain gorillas have longer palates than the Coast gorillas. The "averages" indicate a significant grouping. The curve brings out the fact that the Western Cameroon gorilla has a short palate.

4. *Cranial length* (glabella to inion): —

Average		*Curve*	
Gab.	103	Gab.	105
Cam.	98.5	Cam.	100
W. Cam.	94	W. Cam.	95 and 110
Kivu	93.5	Kivu	90–95
E. Mt.	90.5	E. Mt.	90–95

This measurement separates the Gaboon and Cameroons from the Mountain and Kivu gorillas. If any grouping were to be done the Western Cameroons would be with the Mountain gorillas. The Western Cameroons show two distinct peaks.

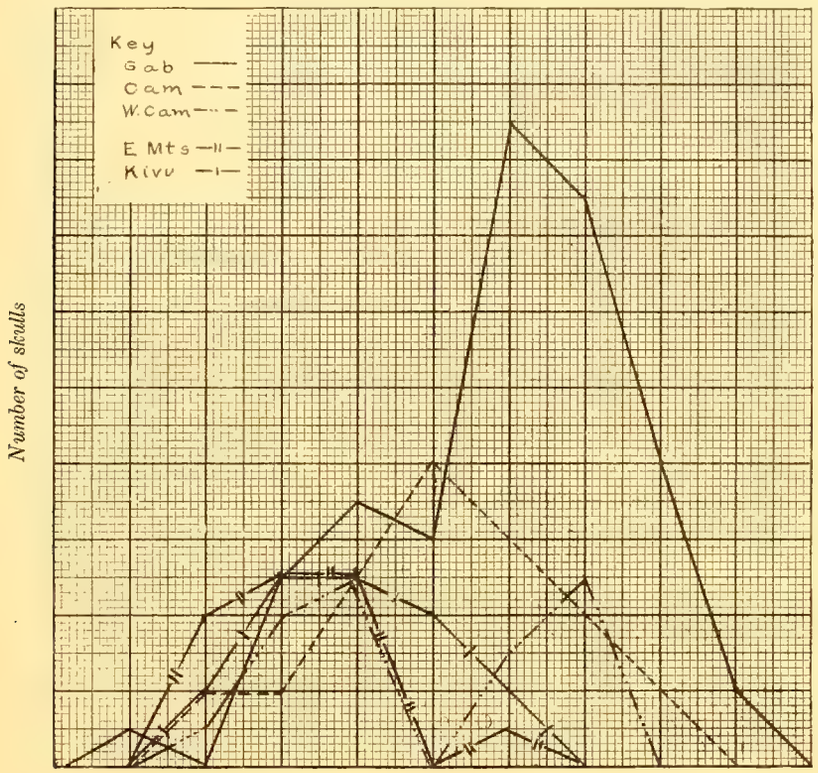

FIG. 3.— Cranial length, glabella to inion.

5. *Length of rostrum* (gnathion to nasion): —

Average		*Curve*	
Gab.	64.5	Cam.	70 (M) and 66 and 58
Cam.	64.5	E. Mt.	66
E. Mt.	64.5	Gab.	63
W. Cam.	61.5	W. Cam.	66 and 58 (M)
Kivu	59	Kivu	58–64

This measurement shows a great many peaks in the curves and indicates that the Eastern Mountain and Cameroons gorillas are long-faced, while those from the Kivu have the shortest faces.

6. *Basion-nasion* (third side of facial triangle): —

Average		*Curve*	
Gab.	71	Gab.	72
W. Cam.	69.5	W. Cam.	70
Cam.	68.5	Cam.	70
Kivu	67	E. Mt.	67
E. Mt.	66	Kivu	66

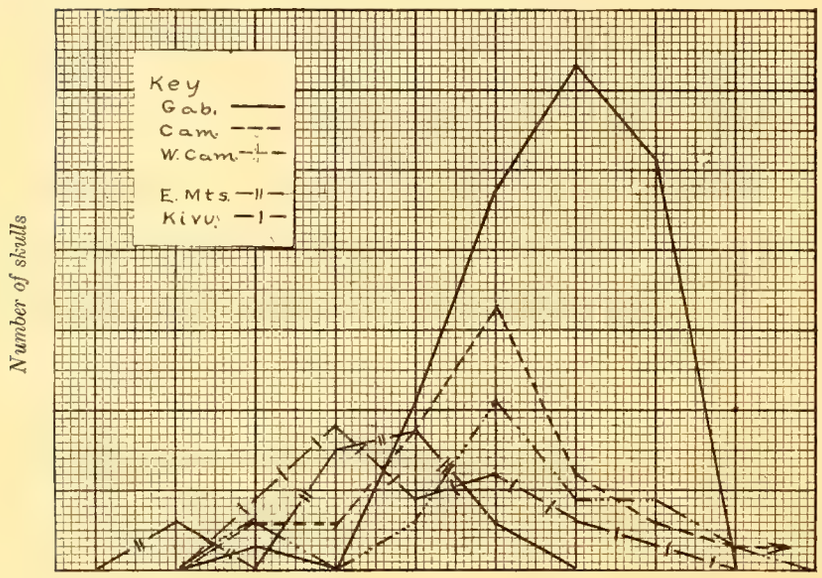

FIG. 4.— Basion-nasion length.

This shows a definite grouping into Coast and Mountain that of itself might be of little significance.

7. *Height of occiput* (upper border foramen magnum to inion): —

Average		*Curve*	
Gab.	50	Cam.	54
W. Cam.	49.5	W. Cam.	52
Cam.	49	E. Mt.	52
E. Mt.	48	Gab.	50
Kivu	46.5	Kivu	46

There are so many peaks in the curves that this measurement seems of little significance other than showing that the Kivu gorilla has the shortest occiput.

8. *Zygomatic width:* —

	Average		*Curve*
Gab.	91.5	Gab.	95
W. Cam.	91.5	W. Cam.	95
Cam.	91	Cam.	95–90
E. Mt.	85.5	E. Mt.	85–90
Kivu	85	Kivu	85–90

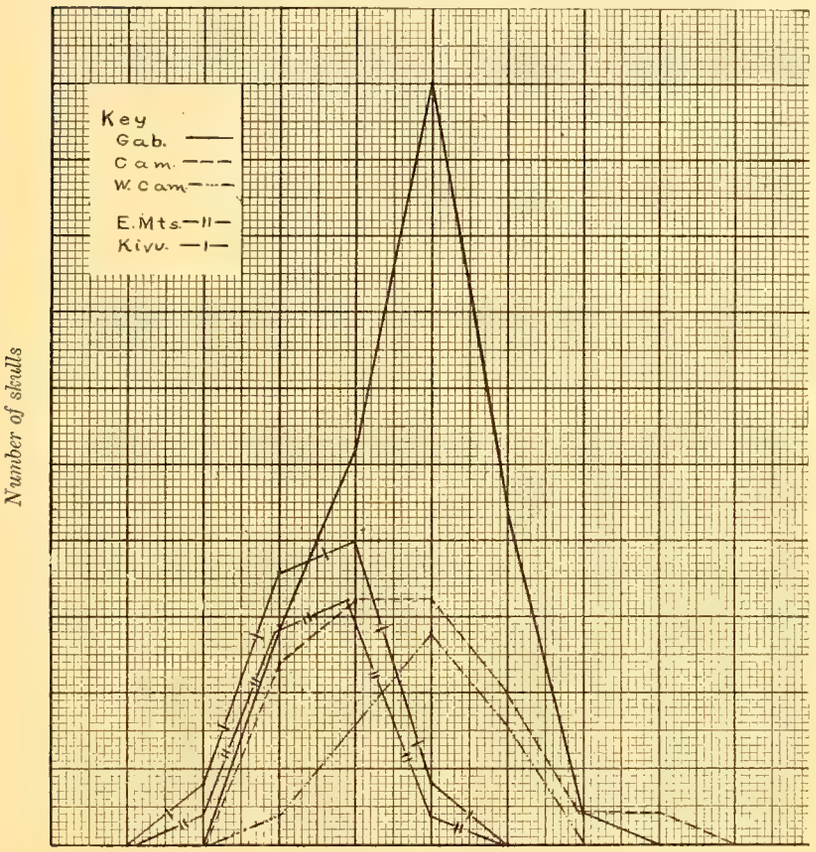

FIG. 5.— Zygomatic width.

This seems to indicate division into two groups, the Coast and the Mountain.

9. *Mastoid width:* —

Average		*Curve*	
W. Cam.	83	Gab.	85
Cam.	82	Cam.	85
Gab.	81.5	W. Cam.	85
Kivu	77	Kivu	80
E. Mt.	74.5	E. Mt.	80–75

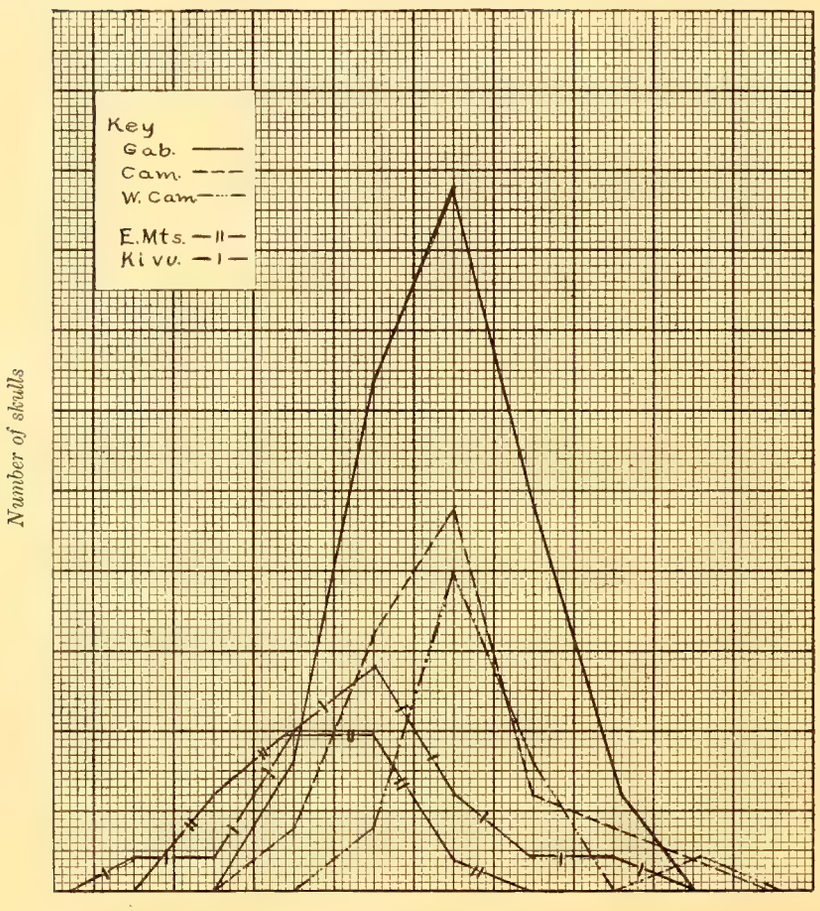

FIG. 6.— Mastoid width.

This seems to indicate a division into two groups, the Coast and the Mountain.

10. *External cranial width* (greatest width on parieto-squamosal suture): —

	Average		*Curve*
Gab.	54	Gab.	55
Cam.	52.5	Cam.	55
W. Cam.	52	W. Cam.	55
Kivu	49.5	Kivu	50
E. Mt.	47	E. Mt.	50

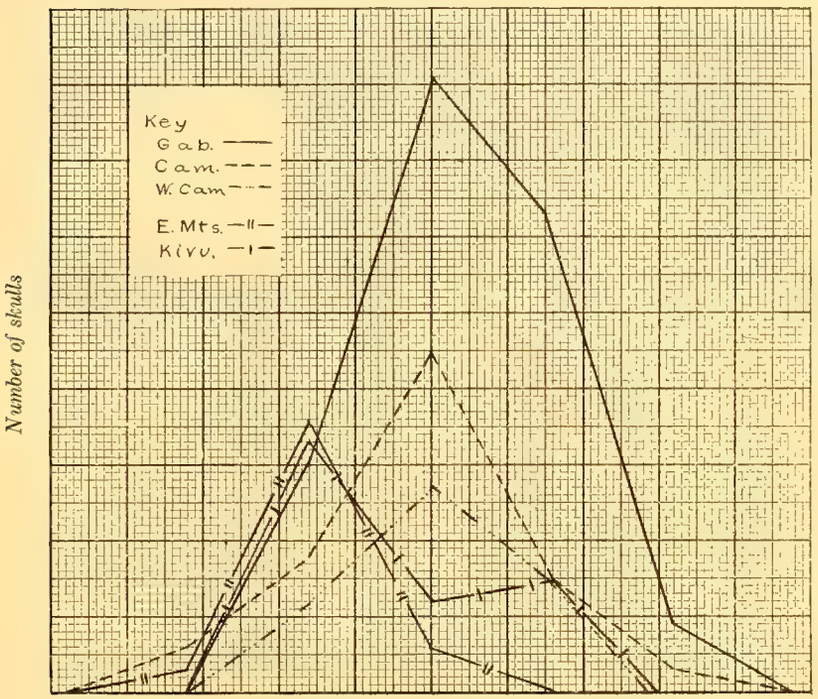

FIG. 7.— External cranial width.

This seems to indicate a division into two groups, the Coast and the Mountain.

11. *Orbital width* (distance across orbital cavities): —

	Average		*Curve*
W. Cam.	58.5	W. Cam.	60
Cam.	58	Cam.	58
Gab.	57.5	Gab.	58
Kivu	53	Kivu	56
E. Mt.	52.5	E. Mt.	50 and 54–56

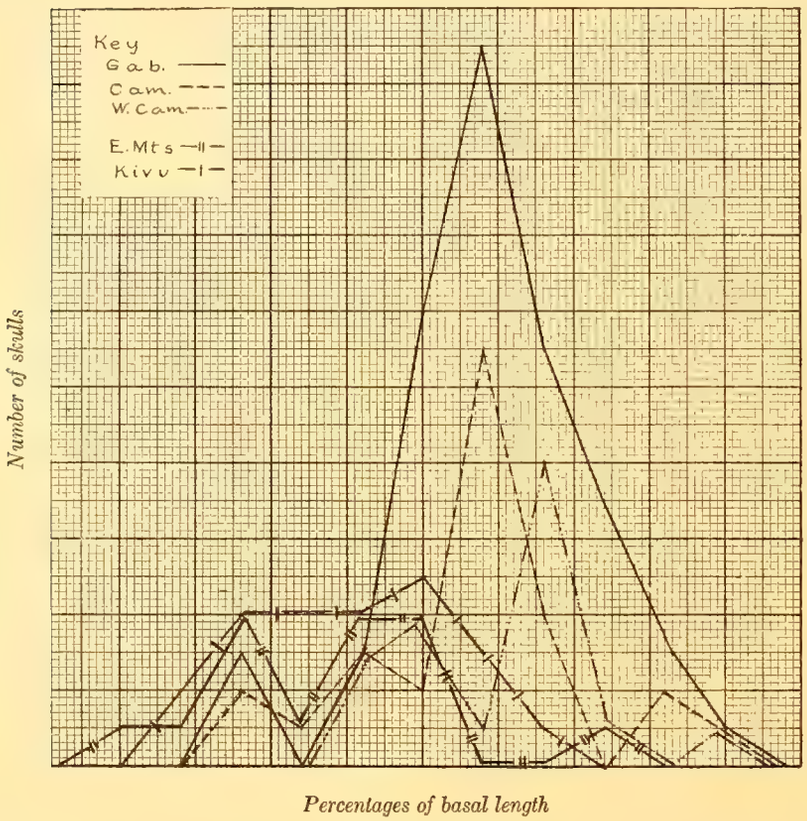

FIG. 8.— Orbital width.

These measurements seem to show a grouping of the Coast and the Mountain gorillas.

12. *Cranial height* (distance between basion and point where sagittal crest forks in front): —

Average		*Curve*	
Gab.	58	Gab.	58
Cam.	58	W. Cam.	58
W. Cam.	58	Cam.	56 (M) and 60
Kivu	55.5	E. Mt.	56
E. Mt.	55.5	Kivu	54–56

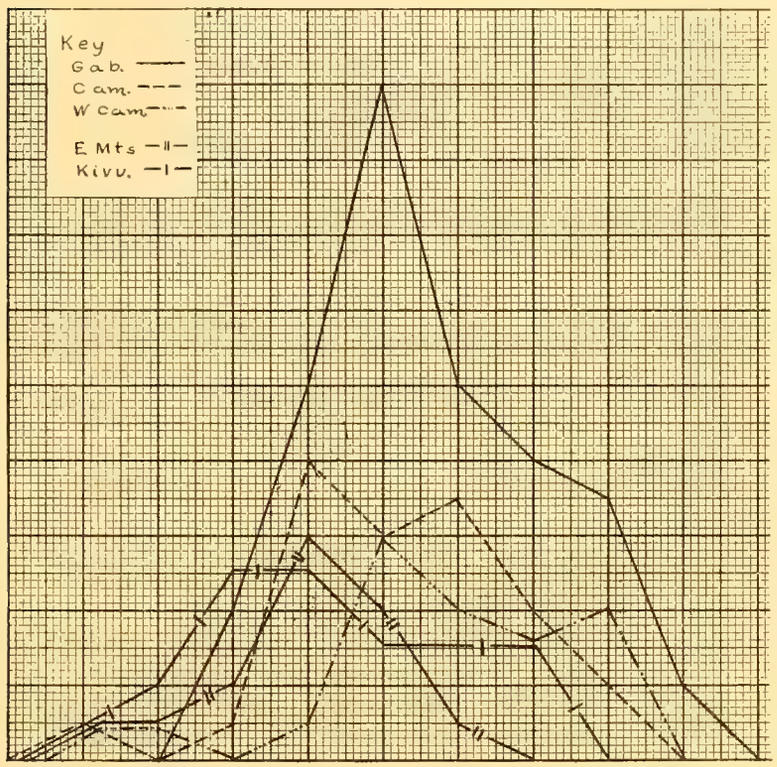

FIG. 9.— Cranial height.

The average certainly and the curve to a less degree seem to divide the Mountain and Coast gorillas into two groups.

13. *Sagittal arc* (a special measurement to show variation in height of sagittal crest). In figuring the per cent of this measurement 50 mm. is used as a base.

Average		*Curve*	
Gab.	199	E. Mt.	250 (M) and 200 (M)
Cam.	192	Cam.	250 and 200 (M) and 125
W. Cam.	190	Gab.	200 (M) and 125
E. Mt.	190	W. Cam.	175
Kivu	180	Kivu	250 and 200 and 125 (M)

This measurement is very variable and little to be depended on. The curve groups the skulls for certain heights of crests in such a way that very few bridge the gap between the groups.

When the curve is made, by using the percentages of basal length as with the other measurements, we find: —

	Curve
Kivu	34 (M) and 50
Gab.	34 and 50 (M) and 60
W. Cam.	45 (M) and 54–61
Cam.	50
E. Mt.	55

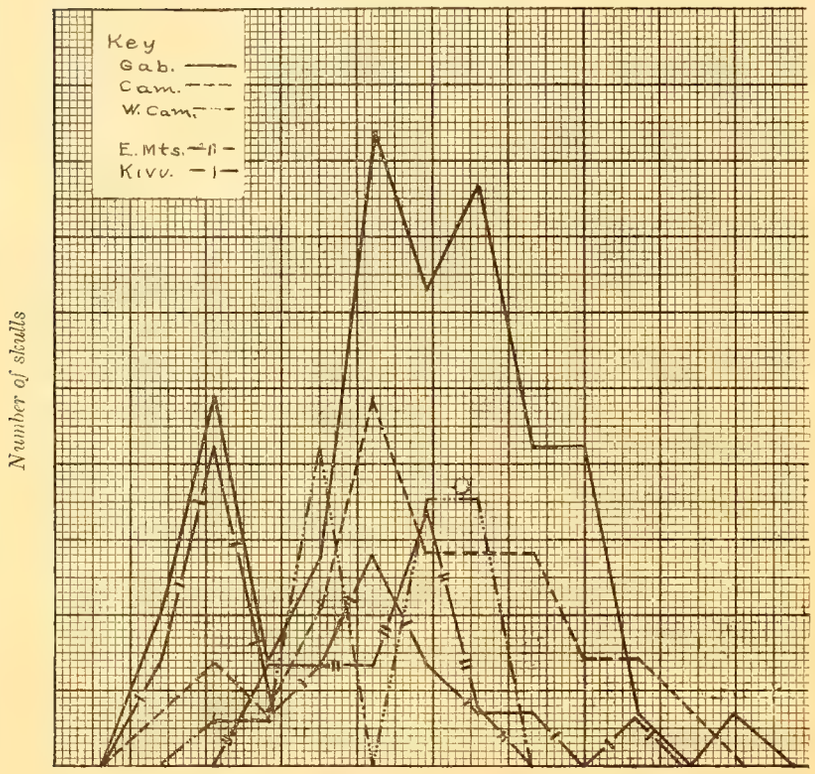

FIG. 10.— Height of sagittal crest.

This shows great variation but a rough correlation or similarity exists between this and the orbital-arc curve.

14. *Orbital arc* (a special measurement to show variation in cross-section of orbital ridge). In figuring the percentage of this measurement 50 mm. was used as a base:—

Average		*Curve*	
Gab.	151	Gab.	150
Cam.	150	Cam.	140
W. Cam.	144	W. Cam.	140
E. Mt.	140.5	Kivu	140
Kivu	138	E. Mt.	140

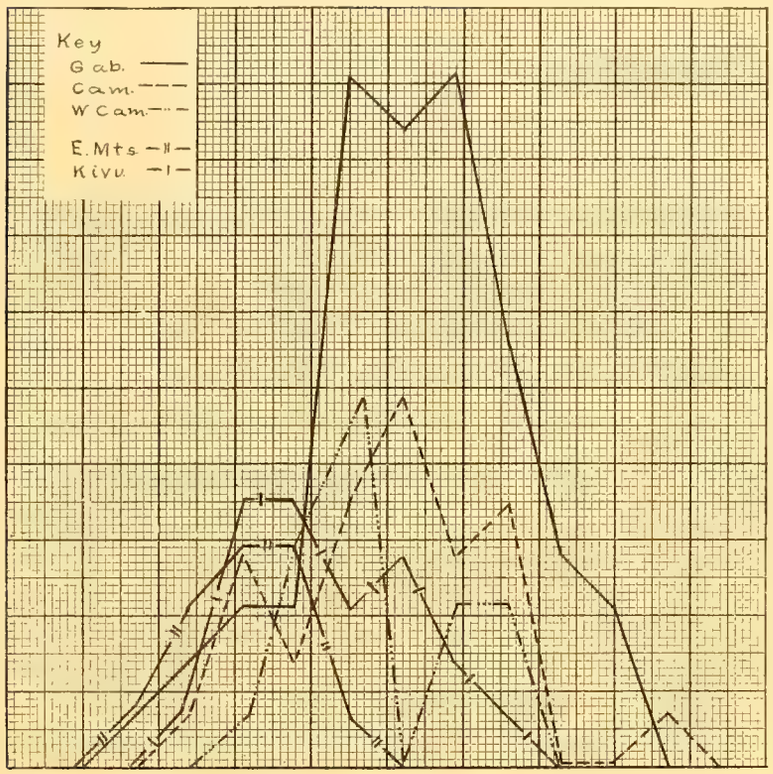

FIG. 11.— Width of orbital arc.

There are many peaks in the curve. This measurement is very variable and little to be depended on. It shows that Gaboon gorillas tend to have most prominent orbital ridges. The averages show less crest for the Mountain and more for the Coast, with the Western Cameroons as intermediate.

When this curve is made by using percentages of the basal length, as in the other measurements, we find: —

Curve	
Kivu	34–36
E. Mt.	34–36
W. Cam.	38 (M) and 42–44
Gab.	38 and 42
Cam.	40

This shows great variation but a rough correlation or similarity exists between this and the sagittal-arc curve.

MANDIBULAR MEASUREMENTS.

15. *Outside intercondylar width:* —

Average		*Curve*	
Gab.	74.5	Gab.	76
W. Cam.	74.5	Kivu	76 (M) and 72
Kivu	74	Cam.	72
Cam.	73	W. Cam.	73
E. Mt.	65.5	E. Mt.	70

This shows little of significance other than that the Eastern Mountain is markedly narrower than the others. The curves have many peaks.

16. *Outside intercoronoid width:* —

Average		*Curve*	
W. Cam.	65.5	W. Cam.	70
Gab.	64	Gab.	65
Cam.	62.5	Cam.	65
E. Mt.	56.5	E. Mt.	60
Kivu	55	Kivu	60

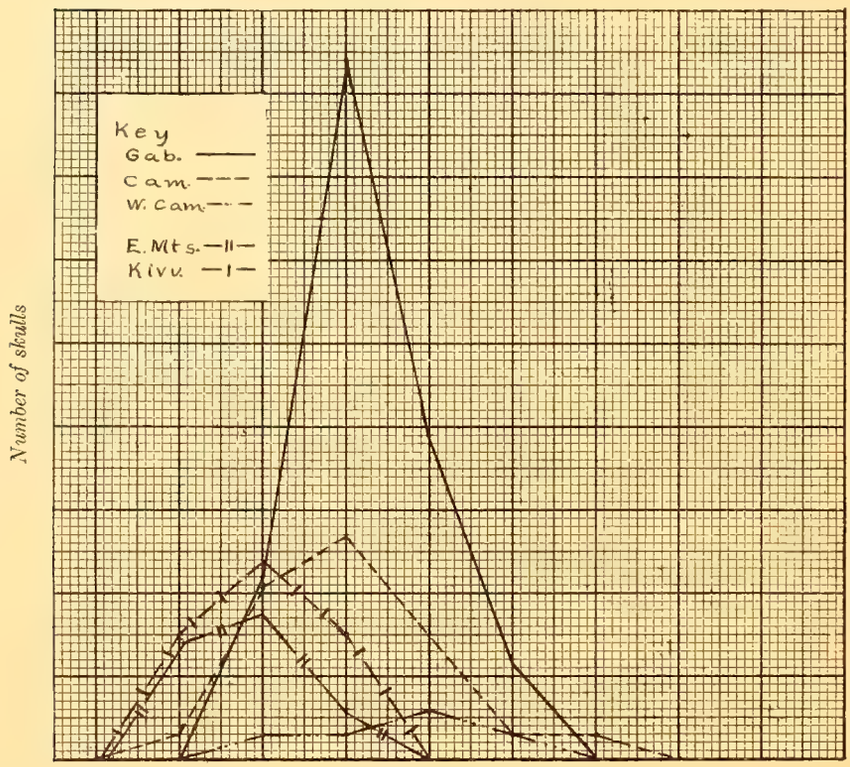

FIG. 12.— Outside intercoronoid width.

This shows a definite grouping into Coast and Mountain forms. The extreme intercoronoid width of the Western Cameroon gorilla is worth noting.

17. *Greatest width across jaws posteriorly:* —

	Curve
E. Mt.	70 and 66
Kivu	66
W. Cam.	68 and 64
Gab.	63.5
Cam.	62

A very variable measurement; shows that Kivu and Eastern Mountain gorillas have a slightly greater width than others, with Western Cameroons intermediate.

18. *Height of ascending process of ramus:* —

Average		*Curve*	
W. Cam.	63	Gab.	70 (M) and 60
Gab.	62	Kivu	65–60
Cam.	61.5	W. Cam.	65 (M) and 55
Kivu	61	Cam.	60
E. Mt.	60	E. Mt.	60

This shows general variation. It is important to note that a small group of Western Cameroons has a much shorter one than the others.

19. *Greatest anteroposterior length of ascending process of the ramus:* —

Average		*Curve*	
Cam.	38	Cam.	40
Gab.	38	Gab.	40
E. Mt.	38	E. Mt.	40
W. Cam.	37	W. Cam.	38
Kivu	36	Kivu	36

Measurement remarkably uniform. It is noticeable that Kivu ramus is slightly narrower than the others.

20. *Condylar width* (greatest transverse diameter of single condyle, usually the left one): —

Average		*Curve*	
W. Cam.	19.5	Gab.	30
Cam.	19	Cam.	20–18
Gab.	18.5	W. Cam.	20–18
Kivu	18	Kivu	18
E. Mt.	17	E. Mt.	18

This shows considerable variation for such a small measurement and the grouping of Coast and Mountain suggested by the curve is by itself of little significance.

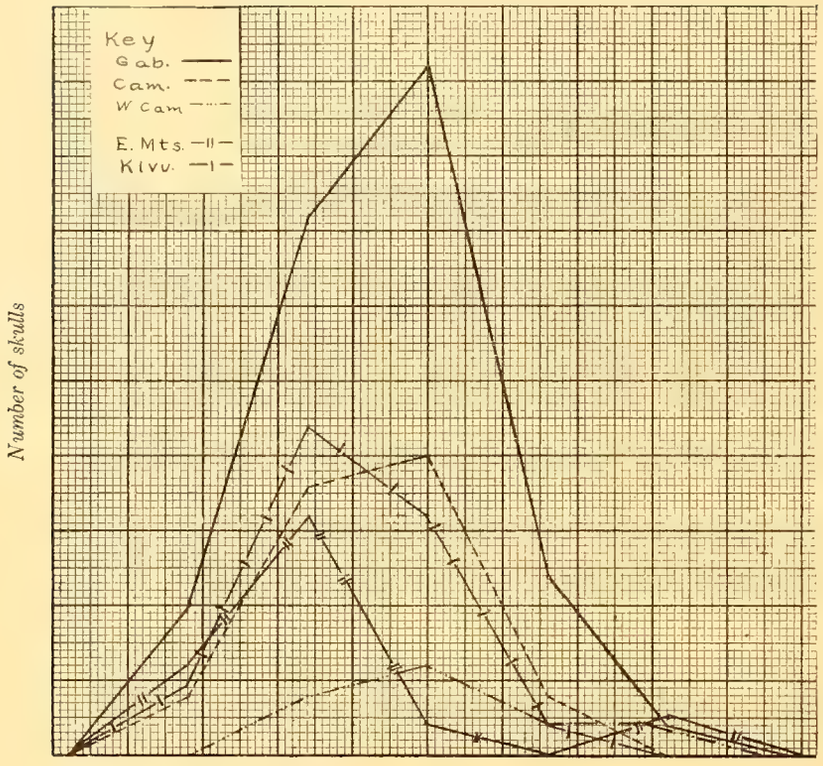

FIG. 13.— Condylar width.

TOOTH MEASUREMENTS.

21. *Length of upper tooth row:* —

Average		*Curve*	
Kivu	46	Kivu	48
Gab.	45	Cam.	48–46
W. Cam.	45	W. Cam.	48–46
Cam.	44.5	Gab.	44
E. Mt.	44	E. Mt.	44

These measurements show a remarkable uniformity. The Kivu gorillas seem to have the longest tooth row.

22. *Length of lower tooth row:* —

Average		*Curve*	
Cam.	49.5	Cam.	52–48
W. Cam.	49.5	W. Cam.	52 and 48
Kivu	49.5	Kivu	52 and 48
E. Mt.	49	E. Mt.	50
Gab.	48.5	Gab.	50

This measurement shows a remarkable uniformity.

23. *Outside alveolar width* (upper jaw): —

Average		*Curve*	
Gab.	37.5	W. Cam.	40–36
Cam.	37	E. Mt.	38
W. Cam.	37	Cam.	38
E. Mt.	37	Gab.	38
Kivu	35.5	Kivu	36

Remarkable uniformity, with Kivu the narrowest.

24. *Outside alveolar width* (lower jaw): —

Average		*Curve*	
Cam.	33.5	Cam.	34
Gab.	33.5	Kivu	34
E. Mt.	33.5	E. Mt.	34
Kivu	33.5	Gab.	34
W. Cam.	32.5	W. Cam.	32

Remarkable uniformity with Western Cameroons the narrowest.

25. *Inside alveolar width* (upper jaw): —

Average		*Curve*	
Cam.	18.5	Gab.	20
W. Cam.	18	Cam.	20
E. Mt.	18	E. Mt.	20
Kivu	18	W. Cam.	20–18
Gab.	17.5	Kivu	18

Remarkable uniformity.

26. *Inside alveolar width* (lower jaw): —

Average		*Curve*	
W. Cam.	20.8	Gab.	22
Cam.	20.5	W. Cam.	22
Gab.	20.5	Cam.	22–20
E. Mt.	19.5	E. Mt.	20
Kivu	17	Kivu	18

Shows narrower palate in Kivu; otherwise remarkable uniformity.

Summary Comparison of Skull Measurements.

In all the twenty-six measurements just recorded there is such uniformity that there are no grounds for doubting that all the gorillas measured belong to one species. The tooth measurements are remarkably similar and suggest no basis for subdivision of the species. The length and width of the ascending branch of the ramus, the length of the occiput, the height of the sagittal crest, all show con-

siderable variation that is very much an individual characteristic, but in no way correlates the skulls into definite groups.

When dealing with the most important measurements, while there is no doubt that all the gorillas belong to a single species, one does find a certain grouping of the skulls within this species. The curves that represent these more important measurements all overlap each other, which shows an intergradation, but the peaks of the curves do not necessarily coincide. They show a distinct division into two groups: the Kivu and Eastern Mountain making up one group, and the Cameroons, Gaboon, and Western Cameroons representing the other group.

By way of summary, the following important measurements indicate a division into two groups, the Coast and the Mountain gorillas. These measurements overlap, but nevertheless show a significant difference in their averages.

The greatest total length — Coast longer, Mountain shorter.
Palatal length — Coast shorter, Mountain longer.
Zygomatic width — Coast greater, Mountain lesser.
Mastoid width — Coast greater, Mountain lesser.
External cranial width — Coast greater, Mountain lesser.
Orbital width — Coast greater, Mountain lesser.
Outside intercoronoid width — Coast greater, Mountain lesser.

In all the above, the Coast is the greater, except in length of palate.

The following measurements show the same grouping to a smaller but nevertheless noticeable degree.

Basion-nasion — Coast longer, Mountain shorter.
Cranial height — Coast greater, Mountain lesser.
Condylar width — Coast greater, Mountain lesser.

The following tend to group the Mountain gorillas together with usually one group of the Coast gorillas as a sort of intermediate between the Mountain and the other Coast animals.

Basal length — Mountain greater, Cameroons intermediate, Coast lesser.
Cranial length — Coast greater, Western Cameroons intermediate, Mountain lesser.
Orbital arc (average) — Coast greater, Western Cameroons intermediate, Mountain lesser.
Greatest width across jaws posteriorly — Mountain greater, Western Cameroons intermediate, Coast lesser.

It seems as if there were sufficient difference of degree with intergradation to indicate subspecific relationship between the *Mountain* and the *Coast* gorillas.

The following tooth measurements show such uniformity that of themselves they can justify no subdivision of the species.

Length of upper tooth row c–m^3
Length of lower tooth row c–m_3
Outside alveolar width across m^2
Outside alveolar width across m_2
Inside alveolar width across m^2
Inside alveolar width across m_2

The following characters show such an enormous individual variation that they are of no value in subdividing the species: —

Sagittal arc.
Height of occiput.

The following measurements show uniformity, except with respect to one group, that may make them of interest: —

Height of ascending process of ramus, uniform (except in a small group of Western Cameroons gorilla).

Greatest anteroposterior length of ascending process of the ramus, uniform (exception, Kivu ramus slightly narrower than rest).

Outside intercondylar width, uniform (exception, Eastern Mountain the narrowest).

Having tabulated measurements that show no difference in degree and those that divide the skulls into two groups, we may now consider the geographical groups, one by one, and any significant characteristics that are revealed in their curves or measurements.

Under *Mountain* Gorilla: —

Kivu: Height of occiput — shortest.
Greatest anteroposterior length of ascending ramus — least.
Outside alveolar width at m^2 — least.
Length of upper tooth row, c–m^3 — longest.
Sagittal arc — least (lowest crest).
Length of rostrum — shortest.
Eastern Mountain: Outside intercondylar width — least.

Under *Coast* Gorilla: —

Cameroons: nothing.
Gaboon: Cranial length — longest.
Orbital arc — greatest.
Western Cameroons: Palatal length — shortest.
Orbital width — greatest.
Cranial length (divided into two groups, one similar to Mountain, other to Coast).
Intercoronoid width — greatest.
Height of ascending process of ramus — small group from this region have much the shortest.

Under this grouping the Kivu and the Western Cameroons would be the only groups worth considering as possibly separable from the rest. The distinctive

differences are all small and do not seem to be of sufficient degree to justify making either of these groups a separate subspecies in the present state of our knowledge.

Briefly to sum up: — The African gorillas show no differences of kind sufficient to justify the recognition of more than the one original species *Gorilla gorilla* (Savage and Wyman). There does exist, however, a difference in degree not very great, but sufficient to separate the Coast from the Mountain Gorillas. These differences based on average skull measurements give the Coast Gorilla the maximum in greatest total length, zygomatic width, mastoid width, external cranial width, orbital width, outside intercoronoid width, basion-nasion, cranial height, and condylar width; the Mountain Gorilla the maximum in palatal length.

As the type form is the Coast Gorilla and the first-described Mountain Gorilla was *Gorilla gorilla beringei*, it is proper to use the latter name for our Mountain Gorilla subspecies. Undoubtedly some naturalists will distinguish the Eastern Mountain race from the Kivu and will continue to use for it the name *graueri*, and for the Coast gorilla of the Western Cameroons the name *diehli*. However, from a study of the existing specimens of gorillas in the museums of the world, I see no sufficient justification for giving *graueri* or *diehli* the rank of a distinct subspecies.

There exists then only one species represented by two forms: — *Gorilla gorilla gorilla* from the coast and *Gorilla gorilla beringei* found in the mountains of the eastern Congo.

Schultz's Comparative Bone Measurements.

Schultz (1927, p. 31) in his studies on the growth of Gorilla has made the following observation from comparative bone measurements based on thirty-eight adult *Gorilla gorilla*, five adult *Gorilla "graueri,"* and five adult *Gorilla gorilla beringei*.

"The sum of the humerus and radius lengths in percentage of the added lengths of femur and tibia averages in adult Lowland Gorillas 117.1 (with no noteworthy sex difference) and in the Highland Gorillas (*Gorilla beringei*) 112.4. All the individual values of the latter fall below the average of the former, but the ranges of variation in the two groups overlap to a considerable extent. It can be said, therefore, that, whereas there exists no constant specific difference in this respect, *Gorilla beringei* shows nevertheless a clear trend toward having relatively shorter arms, or rather relatively longer legs, than *Gorilla gorilla*. The latter, in this respect, is removed somewhat further from man than is the former. . . . As

will be pointed out later on, a study of the hands and feet in these two types of gorilla leads to corroborative conclusions. *Gorilla graueri* stands in regard to its intermembral index between *Gorilla gorilla* and *Gorilla beringei*, but, though a Mountain Gorilla, its average approaches that of the former more closely than it does that of the latter. . . ."

"In the Mountain Gorilla the thumb seems to have a greater relative length than in the Lowland Gorilla. . . ."

About the length-breadth proportion of the hand from the adults measured by Hartmann and Akeley he says, "Judging by these meagre data *Gorilla beringei* has a relatively broader hand than has *Gorilla gorilla*, and one even broader than have most human beings."

"If it now can be stated that the great toe reaches further in the Mountain Gorilla than in the West African forms, it does not imply that the phalangeal part of this toe is longer in the former than in the latter. From a comparison of the feet of the adults of Akeley and of Brehm on Pl. VI it seems much more likely that the free portion of the great toe is considerably shorter, and hence the metatarsal or tarsal portion relatively longer in *Gorilla beringei* than in *Gorilla gorilla*. . . ."

"The conclusions to be drawn from this discussion of the foot of the gorilla are very similar to those derived from the study of the hand. . . . Some of these features, chiefly the relative lengths of the toes, have not departed so much from the arboreal type in the adult Lowland Gorilla as in the adult *Gorilla beringei*."

In the conclusion under "Body Proportions" we find: "*Gorilla beringei* has on an average somewhat shorter upper and somewhat longer lower limbs than has *Gorilla gorilla*. In Gorilla the forearm is relatively shorter than in any other ape. It is especially short in *Gorilla graueri*, which equals man in regard to the humerus-radius proportion. The hand of the adult gorilla is relatively shorter and broader than that of other apes and equals in these respects the human hand. In regard to the relative size of the thumb the adult gorilla, particularly *Gorilla beringei*, resembles human conditions more closely than do other apes. The foot of the adult gorilla is extremely broad; the heel is broad and prominent; the great toe reaches relatively far forward; and the lateral toes are relatively short. In all these features Gorilla approaches man more closely than do other apes. In *Gorilla beringei* the great toe and the sole extend proportionately further forward than in *Gorilla gorilla* and the cleft between toes I and II as well as the lateral digits are shorter in the former than in the latter."

External Measurements of a Mountain Gorilla.

Adult Male, M. C. Z. 23182

Height, top of skull to heel	1730 mm.
Length, top of skull to end of extended toe	1828
Length of hind foot	300
Height of ear	55
Girth of chest	1574
Top of skull to eyes	240
Top of skull to nose	340
Top of skull to mouth	400
Top of skull to chin	480
Top of skull to ear	170
Top of skull to shoulder	250
Circumference, top of skull around lower jaw	920
Ear to eye	130
Ear to nose	240
Ear to corner of mouth	160
From ear to ear in front	360
From ear to ear in back	380
Ear to shoulder	130
Ear to ear under jaw	580
Width of ear	40
Eye to eye in front	80
Eye to nostril	90
Eye to corner of mouth	120
Eye to chin	200
Eye to eye behind	640
Width of eye	30
Height of eye	13
Width of forehead	150
Height of forehead to top	240
Top of forehead to end of nose	150
Length of nose	50
Width of nose	50
Nose to corner of mouth	120
Nose to top of gum	80
Nose to chin	150
Circumference of head around end of nose	710
Width of mouth, straight	120
Width of upper lip	260
Length top lip to nose	58
Length bottom lip to chin	63
Circumference of head at the mouth	914
Neck to end of chin	136
Neck, length on side	200
Neck, length from solar plexus	250

Neck, circumference	740 mm.
Circumference around the shoulders	2006
Right side	
Length of upper arm, upper side	565
Length of upper arm, under side	394
Length of lower arm, under side	381
Length of lower arm, top side	533
Circumference of upper arm	470
Circumference at elbow	457
Circumference of lower arm	336
Circumference of wrist	305
Hand measurements	
Wrist to end of longest finger	178
Wrist to end of thumb	114
Width of palm	178
Length of palm	178
Length of thumb	51
Length of first finger	76
Length of second finger	102
Length of third finger	89
Length of fourth finger	64
Circumference of palm outside thumb	318
Left side	
Length of upper arm, upper side	—
Circumference of upper arm	457
Circumference at elbow	457
Circumference of lower arm	336
Circumference of wrist	305
Arm pit to thigh bone	717
Arm pit to crotch, in front	1143
Arm pit to crotch, in back	—
Circumference at arm pits	1448
Circumference around belly or waist	1626
Height from solar plexus to crotch	889
Circumference at hips	1499
Length of upper leg, measured on inside	330
Length of upper leg, measured on outside	381
Length of lower leg, measured on outside	355
Length of lower leg, measured on inside	343
Circumference of upper leg, right	610
Circumference of knee, right	470
Circumference of lower leg	336
Circumference of ankle	330
Foot, width at heel	191
Foot, width at ball	178
Foot, length along outer side	305
Foot, length along inner side	279

Foot, circumference of ball of foot	292 mm.
Length of first (big) toe	76–82
Length of second toe	28
Length of third toe	38
Length of fourth toe	44
Length of fifth toe	13
Width across toes	95
Length around end of toes	254
Ankle to end of longest toe	229
From collar bone to solar plexus	368
Distance between nipples	273
Circumference of thumb	82
Circumference of first finger	102
Circumference of second finger	108
Circumference of third finger	95
Circumference of fourth finger	82
Circumference of first toe	108
Circumference of second toe	64
Circumference of third toe	67
Circumference of fourth toe	70
Circumference of fifth toe	79
Top of head to end of tail	1041
Arm pit to end of tail	838
Width of hips	533
Pelvis to anus	305
Arm pit to groin	635
Width of silver band on back	305
Pelvis to knee joint	660
Pelvis to shoulder	660
Neck to anus, front	1168
Length of penis	51
Length of arm	965

Described Species and Subspecies of Gorilla.

The following is a list of recently recognized or described species and races, with their type localities:—

1847. *Gorilla gorilla* (Savage and Wyman). Gaboon, West Africa.
1862. *Gorilla castaneiceps* Slack. Kamma, Fernand Vas, French Congo.
1877. *Gorilla mayema* Alix & Bouvier. Upper Congo (*Pseudogorilla mayema* Elliot).
1903. *Gorilla beringei* Matschie. Kirunga, Ya Sabinyo Volcano, former German East Africa.
1904. *Gorilla dichli* Matschie. Northwestern Cameroons.
1904. *Gorilla gorilla matschiei* Rothschild. Yaundi, Southern Cameroons.
1908. *Gorilla jacobi* Matschie. Mouth of Lobo River, Southwestern Cameroons.

1912. *Gorilla gorilla schwarzi* Auerbach. Northern Belgian Congo.
1914. *Gorilla hansmeyeri* Matschie. Assobam, west of Mkobe, Cameroons.
1914. *Gorilla zenkeri* Matschie. Near Mbiawe, Southwestern Cameroons.
1914. *Gorilla graueri* Matschie. 20 km. northwest of Boko, west of Lake Tanganyika, eastern Belgian Congo.
1917. *Gorilla beringei mikenensis* Lönnberg. Mikeno Volcano, Kirunga Mts., Belgian Ruanda.
1927. *Gorilla uellensis* Schouteden. Bondo, Uele.
1927. *Gorilla rex-pygmaeorum* Schwartz. Luofu, west of Lake Edward, eastern Belgian Congo.
1927. *Gorilla gorilla halli* Rothschild. Spanish Guinea (Punta Mbouda).

No less than fifteen forms of gorilla are thus currently recognized in nomenclature. I plan to take them up briefly, one by one, in their chronological order.

1847. *Gorilla gorilla* (Savage and Wyman) is the first recognized form in nomenclature. It comes from the Gaboon, West Africa. *G. savagei* of Owen, described in 1848, has always been regarded as a synonym, as also Geoffroy's (1853) name *gina*, given to a Gaboon gorilla. This last is based on one of the very first specimens to reach France and Geoffroy was undoubtedly impressed by the differences between it and the original type, even though they both came from the Gaboon, for he had no knowledge of the enormous variation in this group. Mayer's *Satyrus adrotes* (1856) is a renaming of the original gorilla. The specific name *gesilla* Blainville (1849), as Schwarz points out, was a misprint for *gorilla* which was corrected in a later explanation of the plate on which the name occurs (Rev. Zoöl. et Bot. Afr., vol. 16, no. 2, p. 7, 1928).

1862. *Gorilla castaneiceps* Slack. On the basis of a colored cast of the head of a gorilla, Dr. Slack characterized this new species, the principal specific character being the existence on the top of the head of a circular patch of reddish hairs. He also said that the skull presented important differences. I have already shown that red hair is probably a variable and not a specific character. Rothschild writes (1904): "I have seen a good many Gaboon and Ogowe Gorillas and I have found the red color so variable that I am forced to regard *Gorilla castaneiceps* as a casual aberration of *Gorilla gorilla*."

Although it is reported that the original skull can no longer be found, there is a skull in the Paris Museum of Natural History from the type locality and marked as the type of *castaneiceps*. Its measurements seem in no way to justify founding a separate species upon it. While not actually the type, this is probably the skull of the original animal from which the type cast was made.

1877. *Gorilla mayema* Alix and Bouvier. Lord Rothschild (1904) believes this "to be a large ape of the group *Simia vellerosus* (Gray) and not a gorilla at all, although Professor Matschie places it as a synonym of *Gorilla castaneiceps*." Elliot calls this *Pseudogorilla mayema* (Alix and Bouvier). He says: "The genus

has been founded upon the examples seen in Frankfort and not upon the description of Messrs. Alix and Bouvier." These authors state that one of the most remarkable peculiarities of the species consists in the back being covered with very long and thick hair, but Elliot notes that the hair appeared to be no longer on the back of the animals than on other parts. He was unable to find the original skull in Paris. Schwarz (1920) states that the gorillas described by Elliot in the Senckenbergian Museum at Frankfort were only topotypes of *Gorilla gorilla*. This would make *G. mayema* a synonym of *Gorilla gorilla*.

As the original description was based on a female skull and the type skull seems to be lost I see no way of telling whether it is a gorilla or not, and if so whether it has characteristics of a separate subspecies or, as seems most likely, is an ordinary female gorilla with some extreme variation.

1903. *Gorilla beringei* Matschie. In the description of this first specimen of gorilla found in the eastern part of Africa, Matschie makes several distinctive points. The ape has a long thick hairy coat with a strong beard surrounding the face. The nasals are narrow and sharply truncate anteriorly in the direction of the nasal suture, becoming suddenly narrow toward the free border. I have seen this same condition in Coast Gorillas and I have seen Mountain Gorillas in which the naso-maxillary suture forms a shallow curve forward and narrows very gradually toward the free border. Only by the examination of a great deal of material can one sometimes come to realize that what seems an important distinction among a few skulls, namely the shape of the nasals, is really such a nebulous one that it is of little value in classification. Matschie says that the palate is longer than the distance from its posterior border to the anterior rim of the foramen magnum instead of shorter as in West African skulls. Also the superciliary arch is very weak, only 8–9 millimeters at its anterior border, whereas in the others it is at least 11 millimeters thick. This characteristic proves to be such a variable one when dealing with a great many skulls that it is impossible to use it as an important subspecific character. I have mentioned earlier that the lesser orbital ridge is found in the Kivu gorilla.

As this is the first described Mountain Gorilla it is the type of the subspecies *Gorilla gorilla beringei*, and both of Matschie's characteristics of long hair and long palate seem to be important variations from the Coast Gorilla. As Matschie had only one skull for study he was unable to determine the other distinctions separating this gorilla from that of the coast. These I have already mentioned earlier in the paper. Attention has often been called to Elliot's spelling of *beringei* as *beringeri*. In Matschie's original paper (1903) where he names this species he

calls it *Gorilla beringeri*, but since it is named after Captain von Beringe, this is obviously a misprint.

1904. *Gorilla diehli*, described by Matschie, agrees in many measurements, according to him, with skulls from the southern Cameroons. It is in the peculiar form of the posterior part of the cranium that it differs most strikingly. Elliot says: "The type skull of this form is broader and shorter than *G*[*orilla*] *beringeri* with a smaller braincase, but much broader face and shorter rostrum. . . ." I have made tracings of the outside curve of the posterior part of the cranium and find that these gorillas fall well within the range of variation of other Coast Gorillas in this respect. The width of the brain case is usually greater than that of *Gorilla g. beringei*. It seems to have the greatest intercoronoid and interorbital width of any of the Coast Gorillas. Considering the wide limits of individual variation that I have shown earlier in this paper it does not seem to me that there is sufficient difference of degree to make this *Gorilla diehli* a separate subspecies.

1904. *Gorilla gorilla matschiei* Rothschild. The characteristics of this race are: "hair longer than in *Gorilla gorilla*, while back and fore part of legs much grayer, limbs much shorter and stouter, crest of skull generally higher and rising closer to the arcus superciliaris, skull generally shorter, female much grayer." Then a table of comparative measurements is given which brings out the fact that the skull of the type of *Gorilla gorilla matschiei* is a good deal larger than the skulls with which it is compared. The most striking differences are certainly in the shape of the hinder surface of the head and the basi-occipital bone, as well as the very widely different portion of the lower jaw comprising the coronoid process and the articular condyle. I have found that the length of hair and the color of it are neither of them reliable among the Coast Gorillas as a basis of classification. The height of the crest of the skull is so variable that it forms no sound basis for distinction between races. Lord Rothschild's table of comparative measurements shows a variation that falls easily within the range of variation in the gorillas from the Gaboon region alone. I have shown variations of the articular condyle and other parts of the lower jaw which have range enough to include those of *G. matschiei*. My tracings of the occipital region show no characteristics not found in skulls of other Coast Gorillas from different regions when a sufficient number is examined.

Matschie (1905), in discussing this species, finds that the incisor row is wider in the Gaboon than in the Cameroons gorilla. The Cameroons gorilla has the mastoid region less swollen outward, and a shorter face than the Gaboon gorilla.

All these characteristics are lost in individual variation when a large series of skulls is examined.

Matschie, after discussing this new southern Cameroons form, says that, on the other hand, several skulls from the region of Bibindi in Lokundse, southern Cameroons, agree neither with the Gaboon nor with the Sanago basin skulls, but the material available is insufficient to determine if a new form is indicated. This corresponds with Matschie's concept of species. If a gorilla skull differed in a slight way from the described species of the region, he immediately began thinking of it in terms of a new form and when material was sufficient, described it as such. It did not seem to occur to him that the existing species might be too narrowly defined. To illustrate his point of view, I know of a case where a man brought him two skulls of gorillas shot out of the same troop. He not only diagnosed them as different species but persisted in thinking that they came from different localities.

1908. *Gorilla jacobi* Matschie. Matschie reports that the skull of this species differs in its extraordinary size, the superciliary arch which is bowed forward, not up, broad hind portion of the end, and broad face. From *G. matschiei*, the largest species previously known, he says that it differs in the planum nuchale running in a rather pointed course to the protuberantia and in the relatively much shorter face. Unfortunately I did not measure this type but I did study several skulls of *G. jacobi* as classified by Matschie and I have compared the type measurements as given by him. The shape of the superciliary arch and the hind portion of the head seem to be very variable and of little value as specific or subspecific characters. The short, broad face is a characteristic already attributed by Matschie to *diehli*. Without question this is a large gorilla, not unlike many as large or larger from both Cameroons and Gaboon. It shows no characteristics that would not be included in the general individual variations common to the race already discussed. Schwarz (1928) lists this as a synonym of *Gorilla gorilla matschiei*. It happens to resemble the type of that so-called species in more ways than the types of other ones.

1912. *Gorilla gorilla schwarzi* Auerbach. Auerbach describes a large specimen from the South Cameroons. He says it is of the species *Gorilla gorilla schwarzi*, of which Matschie is going to publish a description. The hair and coloring is that of a typical Cameroons gorilla and he makes a comparison of skull measurements with those of the type of *Gorilla gorilla jacobi*, in which the two skulls appear to agree within one millimeter in almost every point. The width and length measurements are a little less in *Gorilla gorilla schwarzi*, but fall well

within the normal range of variation of even a well-localized region. Matschie never lived to publish his description of this species, so Auerbach's must stand the test. There is a reference to this gorilla by Dr. Fritze (Jahrb. Prov. Mus. Hanover, 1911, p. 113).

1914. *Gorilla hansmeyeri* Matschie. The most striking characteristics of the specimen according to Elliot and as confirmed by Matschie are: — color nearly white; large skull about equal in size to that of *Gorilla gorilla matschiei;* "enormous crest . . . commences on forward part of frontal a little behind orbital ridge, rises directly upwards"; brain case comparatively small, longer, narrower and less rounded than in *Gorilla gorilla matschiei;* "orbital ridges very prominent and heavy, with deep depression behind at the farther side of which the crest takes its rise"; shorter and more prominent facial region, rostrum broader anteriorly; "the ascending ramus of the mandible is much wider, but the mandible itself is no longer"; broad bony expansion at rear of skull overhangs occipital region and is not on the same plane.

The main points about this animal are its high crest, large orbital ridges, and nearly white color. The first two are, as shown earlier, far too variable to base classification on, and the color is probably a result of age. The length of the facial region, as also of the ascending ramus of the mandible, varies greatly in individual skulls. In the part of this paper that deals with variation I have tried to show the variation in shape of brain case as proved by Dr. Harris's work and also the extreme variation in the shape of the occipital region. It is almost as great as that of the crest. There seems to be no justification for recognizing a subspecific difference in this gorilla.

1914. *Gorilla zenkeri* Matschie. A black gorilla with the shoulders finely speckled with gray, and with a brownish tone upon the loins and upper part of the thighs. The skull of the type is peculiar because the brain case is very shallow and projects horizontally behind far beyond the lower-jaw articulation. The skull has a long facial region and a long brain case with a low crest. The brain case is wide and rounded.

There is no question but that this skull is a rather extreme variation, for the axis of the brain case is in a more horizontal position than the average. The length of brain case or of face is not unusual and the coloring of hair is of little significance. Very few other skulls have the brain case in quite the same relation to the rest of the skull as this one and as they come from different localities it seems likely that this is a rather extreme case of individual variation.

1914. *Gorilla graueri* Matschie. Matschie describes this as a smallish gorilla,

black with light brownish-gray wash, thick beard, very long hair on the arms. Old male has a broad, sharply marked, silvery-white band across the back. The superciliary arch is in the adult more than ten millimeters high, nasal bones cover the entire width of the dorsal border of the nasal opening. Upper incisor row is forty-two millimeters long and occipital condyle is twenty-three millimeters long; otherwise very similar to *Gorilla beringei.*

The shape of both the superciliary arches and the nasals is very variable in gorilla skulls. Only by the most careful comparison can one detect even the distinctions between *Gorilla graueri* and *Gorilla beringei.* Considering the range of individual variation, the types resemble each other remarkably well. Lönnberg, in his 1917 paper, compares his *G. b. mikenensis* first with *graueri,* then with *beringei.* His subspecies is smaller than *graueri* and lacks the red at the tips of the hairs. Even with the additional information supplied by Matschie to Lönnberg about *graueri* it is utterly impossible to find any distinction that is not easily included in the normal range of variation of the Mountain Gorilla.

1917. *Gorilla beringei mikenensis* Lönnberg. Gyldenstolpe (1928) working over the additional collections of gorilla material at the Stockholm Museum says: "The race described by Lönnberg in 1917 as *Gorilla beringei mikenensis* must — at least according to my view — be regarded as a synonym, being evidently only based on individual or perhaps on family variation." He then goes on to compare, point by point, the small differences supposed to separate the two races and I agree absolutely with his conclusion that the majority of the distinctive characters do not hold good when a larger amount of material is examined.

1927. *Gorilla uellensis* Schouteden. This is based on three skulls reported to have come from Bondo on the Uele River, a region where at present gorillas are unknown but which lies between the range of those on the Coast and those found in the Mountains. No description exists other than the following from Schwarz (Rev. Zoöl. Afr., vol. 14, p. 335, 1927): "Le passage aux formes occidentales est complêté par trois crânes, du musée du Congo, provenant de la region du Bondo, dans l'Uele (Lemarinel) chez lesquels les arcs superciliaires sont bien plus saillants et ne diffèrent plus que peu du type occidental, tandis que les frontaux sont moins bombés. La description plus précise de ces crânes sera donnée ailleurs. . . . (Note du Dr. Schouteden: Il s'agit du *G. uellensis* Matschie.)" These skulls were procured from the natives of this region and they are well smoked from fire. The square orbital ridge and the high crest with a comparatively narrow brain case are the most striking characteristics, but none of these would justify making it a separate subspecies. In all its measurements it comes

well within the range of variation of the Coast Gorilla, and in having a shorter palate it resembles more closely the Coast than the Mountain form. Undoubtedly at no greatly distant time the ranges of the Coast and the Mountain Gorillas were continuous. It is an interesting thought that the bridge may have been along the Uele. Nevertheless, since these gorillas resemble most closely the Coast Gorilla and since they come from a region not only six degrees west of the Mountain ones, but also four degrees north of the northern limit of the known range of the Mountain Gorilla, it seems possible that they might be skulls from the Cameroons carried in by Arab traders or wandering natives. The locality whence they are reported is on the map only eight hundred and forty kilometers east of the Sanaga River where gorillas are found in the Cameroons. Skulls smoked almost black by native fires, as these are, may last for many years. Although the primitive natives of those parts travel but short distances, some are known to have come down from this region to the Cameroons, hence it is not unlikely that if any of them returned home they might have taken the two female and one male skull in question back with them, for gorilla skulls are much prized by native tribes. My own conclusion is that this supposed species is a Coast Gorilla and if the skull originally came from where it is reported it was probably taken there by some native traveling from the Cameroons.

1927. *Gorilla gorilla rex-pygmaeorum* Schwarz.— "D'apres l'aspect de la pilosité faciale, le nouveau Gorille ressemble à ses deux voisins orientaux et concorde avec *graueri*, dont il se distingue par la fourrure plus courte, raide et non laineuse. Il se distingue aussitôt de *beringei* par l'absence du capuchon et des long favoris caractéristiques, de même que par le pelâge plus court. D'après le crâne il se range également dans le group oriental; mais les arcs superciliaires, plus accentués, indiquent déjà des rappels des formes de la côte occidentale."

Such characteristics as length of hair and length of beard do not seem to me important as specific characteristics because whenever I measured the length of hair in adult male skins from the same limited mountain regions I found a wide variation. Those in the volcanoes were more hairy and longer-haired than the Eastern Mountain ones. As far as stiffness or curliness of individual hairs is concerned I feel that that is largely dependent on the way the hide is treated. Natives often dry hides in the sun or in front of fires. I studied the hide of the type of *rex-pygmaeorum* and compared it with the other Mountain Gorillas without being able to find a just basis for making it a new subspecies. The important skull characteristics Schwarz emphasizes are the shape of the orbital ridges, the sagittal crest starting well forward, a deep and concave triangle between the

parietal crests, the lambdoid crest large and wide, the nasals wide like those of *graueri* without showing the same convexity or length, the shape of the jugal as in *graueri*. Almost all these points are based on shape of crests or nasals which are the most variable things about the gorilla and cannot be depended on for subspecific differences without more important evidence. The type skull of *rex-pygmaeorum* has a very narrow palate that is not of uniform width but narrows markedly behind. This is a rather unusual variation of which I found a few other cases among Mountain Gorillas. With every appreciation of Dr. Schwarz's paper, I cannot agree with him in making a new subspecies of Mountain Gorilla on the basis of the material available.

1927. *Gorilla gorilla halli* Rothschild.—"Differs from both *Gorilla gorilla* and *G. matschiei* in being paler and of decided liver-brown appearance; arms, shoulders, sides and top of head grizzled brown (*i.e.*, brown intermixed with gray hairs). Back, leg and hind neck mouse grey; back of head pale brown; feet and hands sooty black. Appears to be much shorter in height and much more stockily built, owing to the different proportions of some of the long bones. Hair shorter and sparser." Rothschild gives measurements of humerus, ulna, and femur of *Gorilla gorilla matschiei* and *Gorilla gorilla halli*. The humerus shows a length difference of one millimeter, the ulna of 3.25 millimeters, and the femur of 47 millimeters. Color seems to be of little value in classifying gorillas, as it changes with age and also often varies for reasons that have not been explained. As in skulls, so in proportion of limb bones, we find a great variation in individual gorillas. Lord Rothschild seems to have two rather extreme cases in his *Gorilla gorilla matschiei* and *Gorilla gorilla halli*. In discussing further he says: "The skull of *Gorilla gorilla halli* is at once distinguished from that of *Gorilla gorilla gorilla* by the great width of the occipital region and flat not pointed summit of the crista sagittalis. This subspecies is most interesting because it has the very wide, flat-topped occipital region of the skull found in the 'Mountain gorilla' (*Gorilla gorilla beringeri*) whereas externally it has the shorter pelage and general characters of *Gorilla gorilla gorilla* and *Gorilla gorilla matschiei*."

I have several Cameroons and Gaboon gorillas with wider occipital regions than this skull. I have also many tracings of the occipital region of Coast Gorillas that are even wider and more flat-topped than is this skull. In the chapter on variation I reproduce a few tracings and try to show the fallacy of Lord Rothschild's theory of the importance of the external shape of the occipital region and the pointedness of the summit of the crista sagittalis. This gorilla has to a remarkable degree the form and pelage of the Coast Gorilla.

Simplified Lists of Certain Recent Taxonomists.

Having briefly touched on fifteen "species" of gorillas I give now the already simplified lists of certain investigators who have been working in the same general direction toward a revision of the genus Gorilla.

After the whole matter had gone through a period where English, French, and German taxonomists were describing species from insufficient material, Rothschild in 1906 recognized one species and four geographical races: —

Gorilla gorilla (Gaboon)
Gorilla gorilla matschiei (Southern Cameroons)
Gorilla gorilla jacobi (West Central Cameroons)
Gorilla gorilla diehli (North and Central Cameroons)
Gorilla gorilla beringeri (Kirunga, German East Africa)

Elliot's Review of the Primates (1912) gives us one species and eight subspecies, also a Pseudogorilla: —

Gorilla gorilla (Gaboon)
Gorilla gorilla matschie (Yaundi, Southern Cameroons)
Gorilla gorilla diehli (Northern Cameroons)
Gorilla gorilla jacobi (Mouth of Lobo, Southern Cameroons)
Gorilla gorilla castaneiceps (Kamma, Fernand Vas, French Congo)
Gorilla gorilla (later described by Matschie as *hansmeyeri*) (Assobam, West of Mkobe)
Gorilla gorilla (later described by Matschie as *zenkeri*) (Mbiawe, Southwestern Cameroons)
Gorilla beringeri (Kirunga, German East Africa)
Pseudogorilla mayema (Upper Congo)

E. L. Trouessart in 1920 (Bull. Mus. d'Hist. Nat. Paris, vol. 26, pp. 103, 191) writes: "En résumé les specimens que possede le Muséum de Paris indiguent dans la region maritime du Congo français, la presence de deux espèces de gorille, l'une au nord de l'estuaire du Gabon, l'autre au sud de celle large echancrure de la côte, et s'étendant jusqu'au Fernan-Vaz et à l'Ogoove. Les specimens de l'Est Africain ayant servi à l'excellente description de M. Lönnberg prouvent l'existence dans cette region d'une troisième espèce bien distincte. Quant aux formes décrites par M. Matschie (trois du Caméroun et une du Tanganyika) ne les connaissant pas en nature, je crois preferable de ne pas en parler ici."

West Africa: —
Gorilla gorilla
Gorilla gorilla castaneiceps
Gorilla gorilla diehli
Gorilla gorilla matschiei
Gorilla gorilla jacobi

East Africa: —
Gorilla gorilla beringeri
Gorilla gorilla graueri (Tanganyika, 1914)
Gorilla beringei mikenensis (Mikeno, 1917)

Lord Rothschild (1923) realizes that certain Coast Gorillas are dimorphic, so he classifies them as follows: —

Gorilla gorilla gorilla (Gaboon)
Gorilla gorilla diehli (Cameroons)
Gorilla gorilla beringeri (Mountain)

In addition we have: — form. dimorph. *castaneiceps* and *Gorilla gorilla diehli* form. dimorph. *matschiei.*

Schwarz in 1928 (Rev. Zoöl. Afr., vol. 16, pt. 2) lists the following: —

1. *Gorilla gorilla gorilla* (Savage and Wyman) (1847).
   Syn. *savagei* Owen (1848); *gesilla* Blainville (1849); *gina* E. Geoffroy (1852); *adrotes* Mayer (1856); *castaneiceps* Slack (1862); *mayema* Alix and Bouvier (1877); *halli* Rothschild (1927).
2. *Gorilla gorilla matschiei* Rothschild, 1904.
   Syn. *jacobi* Matschie (1906); Schwarz, Auerbach (1912); *hansmeyeri* Matschie (1914); *zenkeri* Matschie (1914).
3. *Gorilla gorilla diehli* Matschie (1904).
4. *Gorilla gorilla uellensis* Schouteden (1927). (Bondo, upper Uele.)
5. *Gorilla gorilla rex-pygmaeorum* Schwarz (1927). (Lubero, eastern Congo.)
6. *Gorilla gorilla graueri* Matschie (1914).
7. *Gorilla gorilla beringei* Matschie (1903).
   Syn. *mikenensis* Lönnberg (1917).

According to my own revision: —

Genus Gorilla

1. *Gorilla gorilla gorilla* (Savage and Wyman), 1847 (Coast).
2. *Gorilla gorilla beringei* Matschie, 1903 (Mountain).

GEOGRAPHICAL DISTRIBUTION.

The gorillas of Africa are found in two limited equatorial regions, separated by a section of the Upper Congo basin that extends from 16° east to 29° 45′ east. The greater part of this intermediate region is covered with dense equatorial forest and, with the exception of three skulls reported as found in a native hut near Bondo, 23° 50′ east on the Uele River, we have no authentic evidence that gorillas exist there. The skulls referred to are similar to those of the Cameroons and might well have been carried over by natives. For convenience in distinguishing the two groups, I shall again refer to the western ones as the Coast Gorillas, even though most of them live at some distance from the Atlantic and some inhabit a mountainous region. The eastern ones are largely found in the highlands of the eastern Congo and will be called the Mountain Gorilla (although my friend, Major Collins, shot one at an altitude of a little over two thousand feet near Walikale).

The distribution of the two groups can be seen by referring to the maps accompanying this memoir.

The limits of the range of the animal on the coast have been determined largely by plotting in all the places whence skulls that seem reliably labeled have come and outlining this area.

For the Coast Gorilla, the westernmost boundary approximates the Cross River in the southern provinces of Nigeria. The most westerly point actually recorded is Ikom, 8° 40′ east and 6° north. The northernmost point is close to Basho, 9° 25′ east, 6° 7′ north. On the east we have reports from several places such as Wesso and Nola on the Sanaga River. The Sanaga River, about 16° 15′, seems to mark the eastern boundary of the range of the Coast Gorilla. On the southeast the line follows the border of the forest which reaches its southernmost limit at Mayombe on the edge of the Belgian Congo, 5° south, 13′ east. Along the Atlantic coast in most places the forest begins a little way inland. Gorillas have been reported actually on the coast, but generally they are found not closer than thirty miles from the sea. They seem especially plentiful along the Gaboon, Ogowe, Camp, and Sanaga Rivers.

The Mountain Gorilla is found in a comparatively narrow strip of the eastern Congo. Its principal habitat is the mountain forest as distinguished from the lowland forest of the Belgian Congo. Its northern limit is Mulu, 0° 10′ south, 29° 10′ east (Absil and Chapin). We find it as far west as Walikale, 1° 20′ south, 28° 1′ east, where it strays a little into the lowland forest. The eastern limit seems to be close to Kigezi in Uganda, 1° 15′ south, 29° 45′ east. The southern limit is Baraka on Lake Tanganyika, 4° 19′ south, 29° 2′ east. In this entire region the gorillas that are most known and accessible are the troops that inhabit the volcano regions where Akeley died while studying them. Whether they are entirely isolated from contact with outside gorillas at the present time is doubtful and has not yet been established. In the mountains back of Baraka, Boko, Uvira, and Katana large troops have been recently found in the upland forests.

An interesting problem is open to anyone who could devote the time to studying the causes of this surprisingly limited distribution. It may be due to lack of some necessary element of food, to some climatic condition, or to natural obstacles. I feel fairly sure that it is not because the gorilla is sedentary in habits or very limited in numbers.

VARIATION.

Harris's work on endocranial variation.— A very valuable contribution to the study of variation in the endocranial form of gorilla skulls has been made by Dr. Harris (1926). He had at his disposal thirty-five adult male and thirteen female gorilla skulls and has devised a method for rapidly obtaining by radiographic means a breadth-length ratio, for the endocranial aspect of the intact skull. In the series of gorillas studied this ratio ranges from 72.1 to 86.8, a range of the same order that occurs in man. Eight out of the forty-eight skulls proved to be dolichocephalic and these were distinct from the nine leptoprosopic skulls, so that there is no close correlation between these two characters of head-length and face-length. The degree of dolichocephaly in the gorilla is as great as that in man. The auricular height-length ratios, as determined by the radiographic method,

FIG. 14.— Tracings of the occipital outline from above: (left) Southern Cameroons; (center) Eastern Mountain; (right) Gaboon.

show that the gorilla is orthocephalic. The average values of these ratios as compared with those of man are as follows (B = Base, L = Length, H = Height): —

		B : L	H : L	H : B
(Martin)	Man	77.8	68.7	88.5
(Harris)	Gorilla	79.3	62.7	79.4

Harris also shows the extreme variability in relative positions of the multiple foramina. In the leptoprosopic gorillas the two foramina are arranged one almost above the other and in the chamaeprosopic gorillas they are arranged almost side by side. In the intermediate forms the lateral foramen is also inferior to the median foramen and all degrees of obliquity can be seen in the series.

Importance of shape of occipital region.— On examining a large series of gorilla skulls one is struck by the enormous individual variation in the shape and the size of the sagittal crests, the supra-orbital ridges, and the shape of the occiput

(Fig. 14). Bunack in a study of the sagittal crests of anthropoid apes showed a correspondence between the extent of temporal muscles, the size of canines, and the development of the lower jaw. Apart from these he creates a "crest factor"

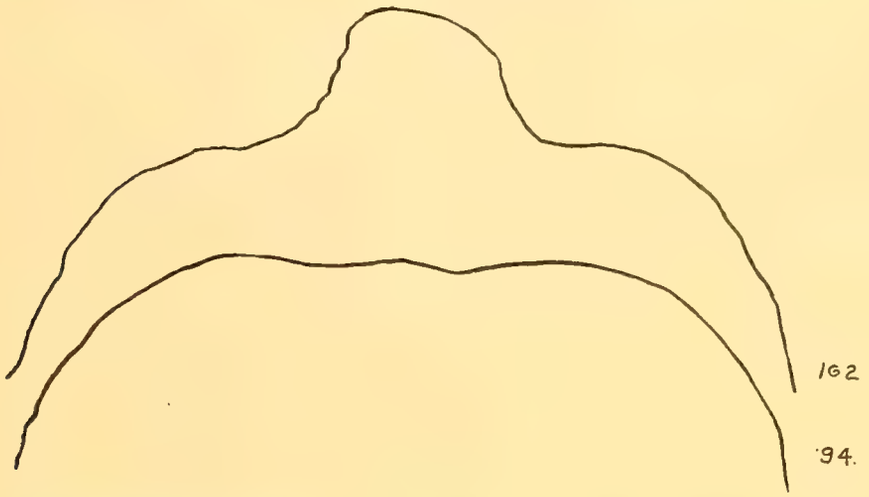

FIG. 15.— Tracings of the occipital outline from above, to show extremes of variation in a single locality (Gaboon).

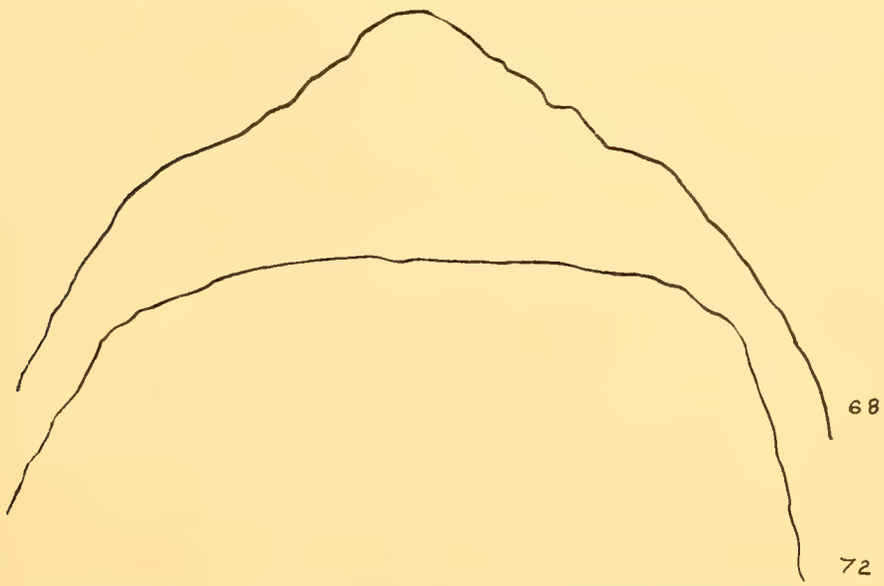

FIG. 16.— Tracings of the occipital outline from above to show extremes of variation in a single locality (Cameroons).

which he calls a systematic character of certain species and subspecies of primates. This same "crest factor" Lord Rothschild has employed in the separation of the species and subspecies. In The Field (July 9, 1922), Lord Rothschild has published figures of three gorilla skulls which are supposed to be distinguished by the

shape of the occiput. He later (1923) says: "The most essential differences of the three races are, however, in the skulls: *Gorilla gorilla gorilla* has the occipital region narrow and appearing almost triangular, owing to the lambdoid crest running up to a sharp point in the centre. *Gorilla gorilla diehli* has the occipital region very broad and the lambdoid crest in the center only rises to a low blunt point. Lastly *Gorilla gorilla beringeri* has the occipital region very broad and the lambdoidal crest is quite flat and horizontal to support the fleshy callosity."

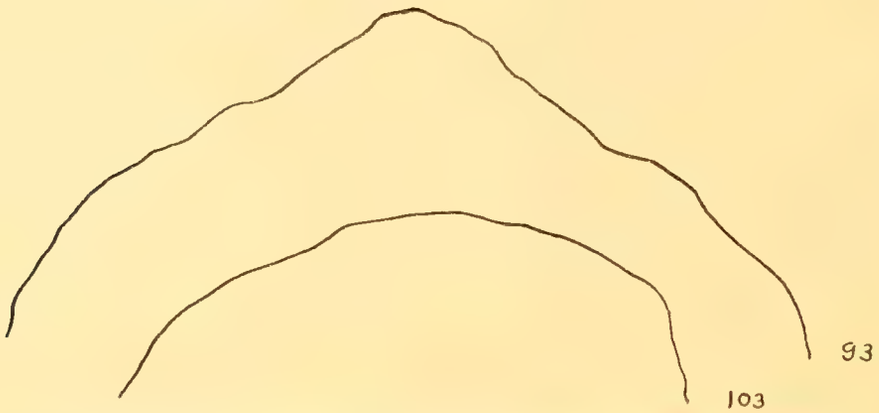

FIG. 17.— Tracings of the occipital outline from above to show extremes of variation in a single locality (Kivu).

Comparative outline tracings of occipital regions.— I have traced the curve of the occiput in over two hundred adult male gorilla skulls and these accompanying outlines (Figs. 15–17) show some of the extreme variations found in skulls from the same regions.

There seems to be little ground for basing classification on the curve of the occiput.

Comparative tracings of orbital ridges.— Another manifestation of extreme variation is seen in the cross-section view of the orbital ridge. This was traced on a fifty-millimeter base from two skulls from the Gaboon that show extremes of variation (Fig. 18).

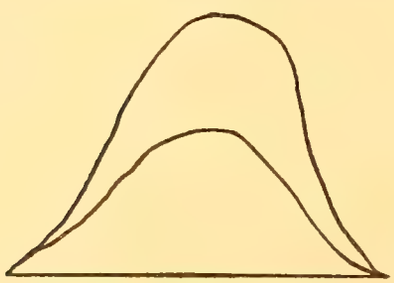

FIG. 18.— Diagram showing extremes in the section of the orbital ridge.

Comparative tracings of sagittal crests.— One of the characteristics most noticeable to one making a comparative study of the gorilla skull is the prominent sagittal crest. While few adult males have the crest almost entirely lacking, this characteristic has sometimes seemed significant enough to bring into a special paper (Bolk, 1925). For comparative

purposes I have outlined the cross-section of the sagittal crest of the skulls used, at a point close to the intersection with the lambdoid suture, using fifty millimeters as a base. The amount of variation appears in the annexed diagram (Fig. 19).

Range of variation in adult skull measurements.— In a study of variation it is interesting to note the range of measurements of the adult gorilla skulls already discussed. They are in terms of percentages of basal length:

Greatest length — Cameroons 126–174
Zygomatic width — Kivu 76–108 Cameroons
Cranial length — Gaboon 79.5–117.8
Cranial width — Eastern Mountain 42.8–66 Cameroons
Cranial height — Gaboon 52.2–65.3
Orbital width — Eastern Mountain 45.6–70.1 Cameroons
Mastoid width — Kivu 62.1–97.5 Western Cameroons
Height of occiput — Cameroons 32.4–62.8 Gaboon
Palatal length — Western Cameroons 52–66.5 Eastern Mountain
(Actual) basal length — Cameroons 160–233 mm. Eastern Mountain
Basion-nasion — Kivu 62.3–85.5 Cameroons
Nasion-gnathion — Kivu 50.8–76.6 Cameroons
Outside intercondylar width — Cameroons 64.5–90.1
Outside intercoronoid width — Kivu 50.2–78.8 Cameroons
Condylar width — Kivu 14.6–22.4 Cameroons; 22.7 (unknown loc.)
Length asc. process of ramus — Kivu 33.2–51.3 Gaboon
Height asc. process of ramus — (Gaboon 51–73.7 Cameroons) (unknown loc. 43.6–74.3)
Greatest width across jaws posteriorly — Gaboon 48–80 Cameroons
Length of maxillary tooth row — Gaboon 37.4–52.7
Outside alveolar width upper tooth row — Cameroons 31.4–42.4, 43.4 unknown loc.
Inside alveolar width upper tooth row — Kivu 15.6–24.7 Gaboon; 25.8 unknown loc.
Length of mandibular tooth row — Western Cameroons 41.3–57.8 Gaboon
Mandibular outside alveolar width — Gaboon 28.5–40.2 Kivu; 42.2 unknown loc.
Mandibular inside alveolar width — Gaboon 13.5–23.9
Orbital arc — Eastern Mountain 28–52 Cameroons
Sagittal arc — Cameroon, Kivu, Gaboon 25–83 (Gaboon, Cameroons)

It is also interesting to see how the extremes of variation balance in the different localities. (As there were more Gaboon skulls, it was to be expected that this group might show the greatest extremes.)

Kivu has 8 Low and 1 High extremes of variation
Eastern Mountain has 3 Low and 1 High extremes of variation
Cameroons has 5 Low and 13 High extremes of variation
Western Cameroons has 2 Low and 1 High extremes of variation
Gaboon has 7 Low and 8 High extremes of variation

These figures suggest many possible interesting explanations.

Variation in skull weight.— Variation seems to be just as great in weight

between different gorilla skulls as it is in such characteristics as height of orbital ridge. In Gyldenstolpe's (1928) table of skull measurements we find that a complete Volcano gorilla skull weights 1964 gr., as compared with the type of *G. beringei* from the same region weighing 1321 gr. Careful weighing of skulls from the same region would reveal an individual variation sometimes greater than the 643 grams just referred to. The Mountain Gorilla, as a general rule, has a lighter skull than the Coast Gorilla.

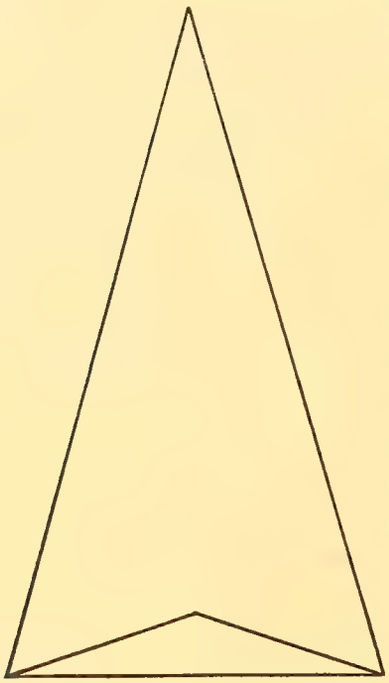

Fig. 19.— Diagram showing extremes in height of the sagittal crest on a base of 50 mm., in skulls from the Cameroons.

Sir Arthur Keith's study of forty-two skulls from one locality.— A valuable contribution to the study of gorilla-skull variation, and significant because it shows for a very limited region what I tried to show for larger areas, has been made recently by Sir Arthur Keith (1927a). After discussing Harris's work on Lord Rothschild's collection, he says: "Thus in the gorilla, which the majority of authorities regard as manifesting a greater structural resemblance to man than any other living form, there is found as wide a range of cranial proportions as is found in any mixed group of human skulls.

"As Lord Rothschild's skulls came from widely separated districts, it was possible that the high degree of variability was due to a mixture of local breeds or races. A collection of gorilla skulls, forty-two in number, which my friend Dr. N. A. Dyce Sharp has presented to the Museum of the Royal College of Surgeons, shows this is not the case; all the skulls come from one locality, where there can be no question of mixture of races, and the variation in them is just as great as that found by Dr. Harris in Lord Rothschild's collection. . . . I have at my disposal forty-seven gorilla skulls from the same area on which to determine the variability in size and shape of the skull. The specimens represent both sexes and all ages, from the full eruption of the first permanent molar teeth upwards. The dimensions of the cranial cavity were taken by direct measurements. . . . In twenty-three skulls of male gorillas from Ossidinge the mean length of the cranial cavity was 121.6 millimeters. The mean width was 95.8 millimeters, the width being thus 78.8 per cent of the length, but there was a range from 72 per cent to 88 per cent—

from pronounced dolichocephaly to ultrabrachycephaly. The mean cubic capacity of seventeen skulls of adult males was 503 cm.^{3}, varying from 355 cm.^{3} to 620 cm.^{3} In a local group of gorilla the brain varies in mass just as much relatively as among members of any human community. . . .

"The degree of variability in gorilla skulls is even more pronounced when external measurements are taken in a manner which gives dimensions comparable with the length and width as usually taken on human skulls. The external length varied, in male skulls, from 113 mm. to 155 mm., the mean being 138.3 mm., while the mean width fluctuated between 92 and 101 mm., the mean being 97.2 mm. The width thus varied from 60 per cent of the length to 79.8 per cent, the mean cephalic index being 66. In female skulls the mean width was 68.6 per cent of the mean length, the proportion varying from 61.7 to 80.6 per cent. There is even a greater variability in the form of the face of the gorilla. In the Ossidinge breed it varies from being short and wide to long and narrow — a variation of a similar kind being also noticeable in all human communities. The Kivu gorilla, which represents the most eastern distribution of the genus, shows the same variability in form of face.

"It is interesting to compare measurements taken on Dr. Sharp's collection of chimpanzee skulls with those taken on gorillas from the same district. In 10 male chimpanzee skulls the cranial capacity varied from 325 cm.^{3} to 430 cm.^{3}, the mean being 368 cm.^{3} The range was thus 105 cm.^{3} compared with 265 cm.^{3} in the male gorilla skulls. In female chimpanzee skulls the capacity varied from 330 cm.^{3} to 395 cm.^{3}, the mean being 358 cm.^{3}, and the range 65 cm.^{3}, compared with 160 cm.^{3} in the corresponding group of gorilla skulls. The mean difference between the capacity of male and female chimpanzee was only 10 cm.^{3}, the sexual difference among gorillas being 76 cm.^{3}"

Some results of Schultz's study on the growth of Gorilla.— Schultz has made a valuable contribution in his recent paper and plates on studies of the growth of gorillas. He makes comparisons of the fetus of anthropoid apes and man, as well as measuring and comparing growth by changes in length or shape of bones.

"In the thirty-eight skeletons of adult *Gorilla gorilla* the humero-radial index ranged from 75.7 to 85.2, the femoro-tibial index from 77.0 to 85.8, the intermembral index from 110.8 to 123.4, the humero-femoral index from 105.8 to 126.3, and the radio-tibial index from 110.4 to 126.0. These wide ranges all indicate a variability which is at least equal to, if not at times larger than the variability of the same proportions in man. Sir Arthur Keith (1926) has recently stated that gorilla varies individually more than does man. Although the writer is not pre-

pared to endorse this view unconditionally, he is convinced that gorilla is at least fully as variable as man. This last conclusion is justified in regard to the limb proportions and undoubtedly true also in regard to the skull of gorilla, as was shown, for instance, by the studies of Selenka (1899), Duckworth (1904), Bolk (1925), and Harris (1926)."

One of Schultz's conclusions that is self-evident after studying his deviation curves is "that the various diverging evolutionary specializations of the higher primates must have affected the limbs much more than the trunk."

"Figure 5, based on Table 10 in this paper, is a diagrammatic representation of the average deviation indices based on the four apes and man for fetuses and for adults. These averages form the radii of the concentric semi-circles and show the comparison at a glance. . . ."

Near the end of the paper Schultz says: "Of all the apes *Gorilla* resembles man most closely, both in fetal and in adult life. . . . Furthermore in the adult of this ape the arms are proportionately shorter and the legs relatively longer than in the young animal. This all rather strongly suggests that, while attaining its unique colossal size, which rendered tree life impracticable, the gorilla swerved in its evolutionary trend toward that which was most likely followed by the human precursors. This change seems to have been somewhat more pronounced, or to have been more accelerated, in *Gorilla beringei* than in the west African gorillas."

Asymmetry.— One of the most interesting variations in the material studied was the distinct asymmetry of a large number of skulls. A. Brazier Howell (1925), in his paper on this subject, discusses it in detail with reference to an adult male Mountain Gorilla, Number 239,883, in the U. S. National Museum. He says that this is due either to an injury or to a diseased condition of the right side of the head at a sufficiently early age so that the bones were still plastic. He then shows and discusses the abnormality. In his conclusion he says: "The primary cause inducing asymmetry in the skulls of mammals other than tooth condition is probably, in most instances, by accident or disease to the bones or muscles of a single side of the head at a comparatively early age and that this must be of such a character as to result in a stunted or infantile condition of a crucial part of the bony framework and a reduction in the rate of growth, or strength, through lesions of the muscles of a single side." In this case we are dealing with a pathological problem.

Gyldenstolpe (1928) says in his recent paper: "A most curious fact that occurs in several of the male skulls is the more or less well marked asymmetry

towards the right of the facial portion of the skull. At least in the majority of these asymmetric skulls neither injuries or old fractures of the bones are to be traced that may have brought about this asymmetry, nor could it be ascertained that it stands in correlation to a more decided wear of the teeth of the right side of the jaws. In the majority of the skulls with worn teeth, those of the right side are, however, mostly somewhat more worn than those of the left."

In the following cases, only a variation of at least two millimeters on either side of the median line is recorded as asymmetrical. Taking the matter up first under the headings of the same regions as used in the earlier discussion of classification we find:

	Right side longest	Left side longest	Both sides even
Gaboon	21	15	25
Cameroons	10	4	15
Western Cameroons	6	8	7
Eastern Mountain	2	6	9
Kivu	6	10	7
Indefinite locality	60	80	102

To sum up: we find from the Coast 37 right, 27 left, and 47 even; from the Mountain 8 right, 16 left, and 16 even. It is interesting to notice that in the Mountain Gorilla the left side is longest almost twice as many times as is the right. In the Coast form, however, the right side is almost one-third more often longer than the left.

In the grand total of 393 skulls we find: right 105 or 28 per cent; left 123 or 31 per cent; even (within 2 millimeters) 165 or 41 per cent. Taking into account the amount of asymmetry on either side, the average for the right side is 3.26 millimeters and for the left 3.70 millimeters. These last figures are based on 228 skulls and this means that the left asymmetries average 0.44 millimeters greater than the right.

Taking the entire group of gorilla skulls the average asymmetrical tendency to the right or left is equal to 2.03 millimeters. This asymmetry seems not easy to explain. In the case of the large majority of gorilla skulls it probably does not result from accident or disease. Some authors suggest that it may be brought about by an uneven development of the brain.

Schultz (1926a) says, in his paper on variability of platyrrhine monkeys, that Mollison (1911) has shown that asymmetries in the length of the limb bones are very common in all primates. He later speaks of Platyrrhini and calls their asymmetries perfectly normal. "There are manifestations of a certain independ-

ent variability in the two halves of the body that are not due to slightly differing functions on the two sides since asymmetries can be very pronounced even in young fetuses."

There is an interesting paper by Hollister (1917) that compares the effects of environment and habit on captive and wild lions. "The skulls of the captive animals are of a definite, uniform shape and differ from all the skulls of wild-killed lions in the Museum collection in a number of conspicuous characters. They are broader and shorter, more massive and bulky, and exhibit abundant relative differences which would be instantly accepted as of 'specific' value in wild animals. The obvious reason for these great differences is that the principal muscles used by a wild lion in mauling and killing game, biting, gripping and striking, have had little influence on the shape of the bones during development. In a wild lion these powerful muscles naturally and in a normal way mold the growing skull, particularly in the regions of their attachment."

In the summary we find: "The skulls of lions and other large carnivores which habitually kill quantities of heavy game are greatly influenced in a definite way by the development of the principal muscles used in gripping, holding, tearing, biting, and shaking. If the animals are captured when young and reared in confinement these particular muscles are little developed and the bone at the region of origin or insertion is little changed by their influence. The bones then retain certain characteristics of juvenility and develop along wholly different but uniform lines from that of the wild-reared animal.

"Changes in the skull which would be accepted as of 'specific' or possibly of 'generic' value in wild animals from different regions are thus produced in the life of a single individual within from five to seven or eight years, almost as rapidly as if by 'mutation.'

"The primary object of this paper is to call attention to a definite case of structural modification by habit."

Conclusions about variation.— In looking at our problem of variation in the gorilla skulls it is impossible to determine how far this variation is caused by muscles developed by their form of living. As in the lions, the feeding habits of gorillas undoubtedly influence the shape of the skull. By way of suggestion: the breaking off of some tough bamboo stalk with the teeth might well be done easier by always pulling in a certain direction and after this was repeated a few times it might become a habit. There may be any number of suggestions as to possible habits of life that would cause variation. To determine what they are is a biological problem of interest to those who may study the "life history of the

gorilla" or the "functional expressions" of some of its structures. In this latter connection Professor R. M. Yerkes of Yale has done some very valuable and in some ways pioneer work with the anthropoid apes, particularly from the psychobiologist's point of view.

It is impossible to come to any final conclusions on this subject until further studies have been made of the growth and development of the animal, as well as the problem of dimorphism. I agree with Gyldenstolpe when he says that the causes of asymmetry (not brought about by accident or disease) are rather obscure and from the material at hand it has not been possible to draw any definite conclusions as to its origin, but I have tried to show the great variability found in this group and to throw out suggestions that may some day lead to a solution of these problems.

Summary.

In 1847 Dr. Thomas Savage, in the Boston Journal of Natural History, gave the first notice of the external characteristics and habits of *Troglodytes gorilla*, regarded as a new species of Orang from the Gaboon River, and Dr. Jeffries Wyman described the osteology of this animal. The latter's conclusions are based on two male and two female skulls, all adult, a male and a female pelvis, the long bones of the upper and lower extremities, and a few vertebrae and ribs. He says (1847, p. 419): "The specific name *gorilla* has been adopted, a term used by Hanno, in describing the 'wild men' found on the coast of Africa, probably one of the species of the Orang."

The taxonomic history of the genus Gorilla has passed through a period which started with Wyman and ended with the death of Matschie, which we may call the old movement to distinguish it from the second period which started with Elliot's Review of the Primates (1912), and which we may call the new movement. In the "old movement" there was a gradual increase in our knowledge of gorillas as new specimens, usually in the form of skulls, drifted into the collections of one country or another, while the English, German, and French scientists vied with each other in describing new species, often with scant material to go on. The leaders of this movement were Paul Matschie in Germany and Lord Rothschild in England.

Movement toward simplification of classification.— The new movement is one that looks upon the variation of gorilla skulls as probably largely individual. The more material that becomes available, the more this idea seems to be confirmed.

Elliot (1912, p. 210), speaking of the three races described from the Cameroons, writes: "With our present material their rank cannot be determined, but the variations shown in the skulls now in the collections, are so considerable that they give no clue towards a settlement of the problem how any kind of distinctive rank can be established. . . . There are probably but two species of Gorillas, so far as our present knowledge permits a decision to be reached. *G*[*orilla*] *gorilla* from the Gaboon, and *G*[*orilla*] *beringeri* from German East Africa. These have little in common with each other, and their widely separated habitats preclude all likelihood of any approach or contact, but the status of the Cameroon Gorillas has yet to be determined. . . . It is however to be expected that many of the variations witnessed in all Gorilla skulls are purely individual, and have little or no real specific value, for like in human skulls, no two crania of these great apes can be found exactly alike, and it is not unlikely when ample material has been obtained that we shall be obliged to modify considerably our present views as to the number of distinct forms of Gorilla that may exist."

Sir Arthur Keith (1927) says: "One other point relating to the differentiation of species among gorillas and chimpanzees may be mentioned here. Lord Rothschild has directed attention to the external characters which distinguish gorillas of one district from those belonging to other districts. There should be no hesitation in distinguishing a gorilla of the western frontiers of Uganda from one native to the eastern frontier of Nigeria, but when I have sought in skulls for recognition marks, I have hitherto failed to find any certain distinctive and constant mark. It is quite true that it is possible in a certain proportion of cases to distinguish the skull of a Kivu gorilla from those from other districts, but for one which can be picked out from a miscellaneous group there are four which cannot be identified, except by their labels. I am sure Lord Rothschild is right in dividing both gorillas and chimpanzees into local races or subspecies, but the degree of differentiation has not yet affected the cranial or dental characters to a degree which permits the racial identification of the majority of individuals."

Gyldenstolpe (1928) says: "As is a well known fact, the skulls of the Anthropoid Apes vary individually to such an extent that hardly a single character can be depended upon. This fact has been further strengthened by the examination of the skulls of the Gorillas from the different mountains of the Birunga Range. This material, which consists of twenty-one specimens, has been collected in a rather limited area from different herds or family parties. As it contains old and adult as well as semiadult and young examples of both sexes, it is rather valuable

for a comparative study of the individual variation among these animals. No skulls — even of those of quite comparable age — are perfectly alike, and they differ from each other in a manner equally great, as has been found among human skulls."

In these quotations Elliot, Keith, and Gyldenstolpe all seem to understand the problem.

In this study I have tried to bring out what seem to me the important specific or subspecific differences found among gorilla skulls in view of the new light and knowledge that we have on the matter of individual variation.

After taking all things into consideration my conclusion is that the gorilla, particularly the adult male, shows a large individual variation even within the limits of a small area; that there is no difference in kind between the Coast and the Mountain Gorillas such as to justify making of them two separate species, but that there is a distinct difference in degree sufficiently important to constitute a subspecific difference between the two groups. While I have reached fairly definite conclusions based on a careful study of all available material, I fully realize that other conclusions may be reached by future investigators when further masses of material have been accumulated.

Revised classification: —

Genus and Species: *Gorilla gorilla*
Gorilla gorilla gorilla (Savage and Wyman) — Coast
Gorilla gorilla beringei Matschie — Mountain

The external characters that distinguish the Mountain from the Coast Gorilla are, besides a longer palate and a generally narrower skull, the thicker pelage, shorter arms and longer legs, large amount of black hair, and fleshy callosity on the crest.

A table of average skull measurements is here appended for the Coast subspecies and the Mountain subspecies.

Average Skull Measurements of Coast and Mountain Gorillas.

	COAST	MOUNTAIN
	mm.	mm.
1. Greatest length	296	292
2. Zygomatic width	179	174.1
3. Cranial length	193	188
4. Cranial width	103.8	98.3
5. Cranial height	114	113.5
6. Orbital width	114	108
7. Mastoid width	159	154.9

	COAST	MOUNTAIN
8. Height of occiput	97	96.6
9. Palatal length	113	125.8
10. Basal length	196	204
11. Gnathion to nasion	124.8	126.3
12. Nasion to basion	136.8	134.8
13. Outside intercondylar width	145	142.5
14. Outside intercoronoid width	125.4	114
15. Condylar width	37.2	35.7
16. Length of ascending process of ramus	73.8	75.6
17. Height of ascending process of ramus	120	123.5
18. Greatest width across jaws posteriorly	124.8	136.8
19. Length of maxillary tooth row	87.8	92
20. Outside alveolar width, upper tooth row	73	74.1
21. Inside alveolar width, upper tooth row	40.6	37.3
22. Length of mandibular tooth row	96.3	101
23. Mandibular width outside alveoli	65.2	68.5
24. Mandibular width inside alveoli	35.3	36.8
25. Orbital arc using a base of 50 millimeters	74	69.7
26. Sagittal arc using a base of 50 millimeters	97	92.5

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EXPLANATION OF THE PLATES.

PLATE 1.

PLATE 1.

Profile view of Mountain Gorilla (photo by T. Alexander Barnes).

HELIOTYPE CO. BOSTON

PLATE 2.

PLATE 2.

Silhouettes of skulls front and side view, showing extremes of individual variation.

Figures 1 and 2, from unknown locality, No. 17–1927 collection of Anatomisches Institute (Dr. Bolk), Amsterdam.
Figures 3 and 4, from Cameroons, No. 41394, collection of Zoologische Museum, Hamburg.

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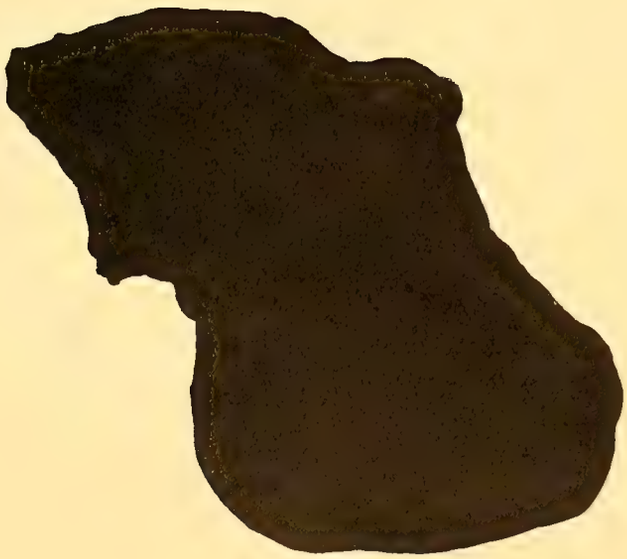

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HELIOTYPE CO. BOSTON

PLATE 3.

PLATE 3.

Silhouettes of skulls, basal, front, and side view, showing degrees of individual variation; all in Congo Museum, Tervueren, Belgium.

Figure 1–3, reported from Bondo, Uele River, north-central Belgian Congo, No. 100.
Figure 4–6, Luofu, eastern mountains, Belgian Congo, No. 8187.
Figure 7–9, Baraka, eastern mountains, Belgian Congo, No. 804.
Figure 10–12, Baraka, eastern mountains, Belgian Congo, No. 999.

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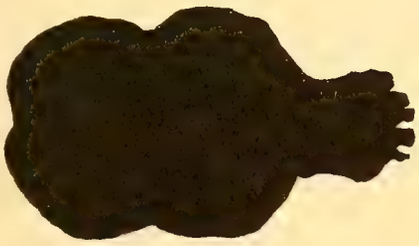

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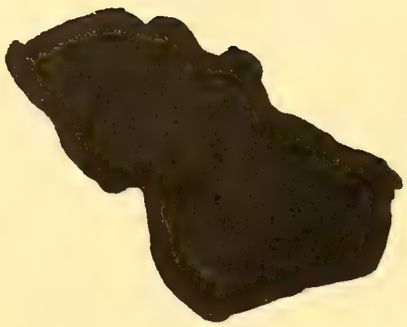

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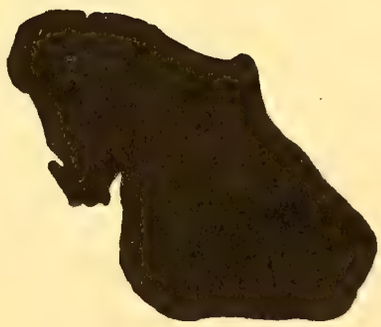

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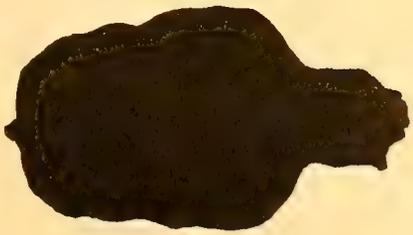
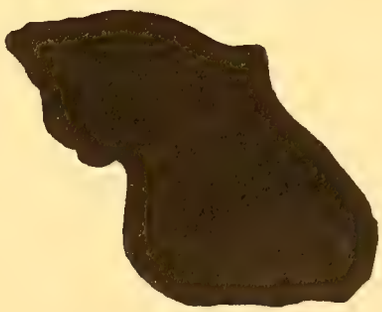


10

11



12

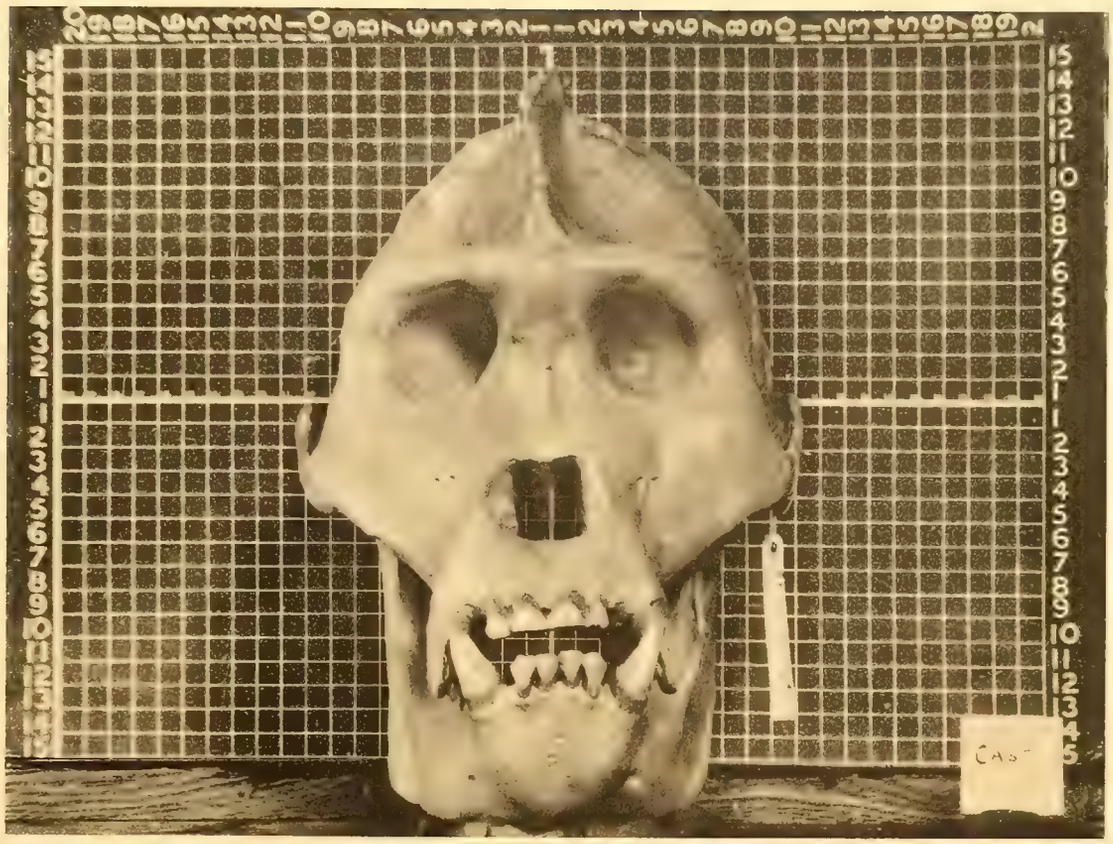
HELIOTYPE CO. BOSTON

PLATE 4.

PLATE 4.

The background screen is divided into centimeter squares.

Front and side view of cast of Gaboon gorilla skull in the Leicester Museum. The cast is in Lord Rothschild's collection at Tring, England. By measurement this is the largest gorilla skull I have found in any collection (No. 147 in my table of measurements). It shows an extreme variation.



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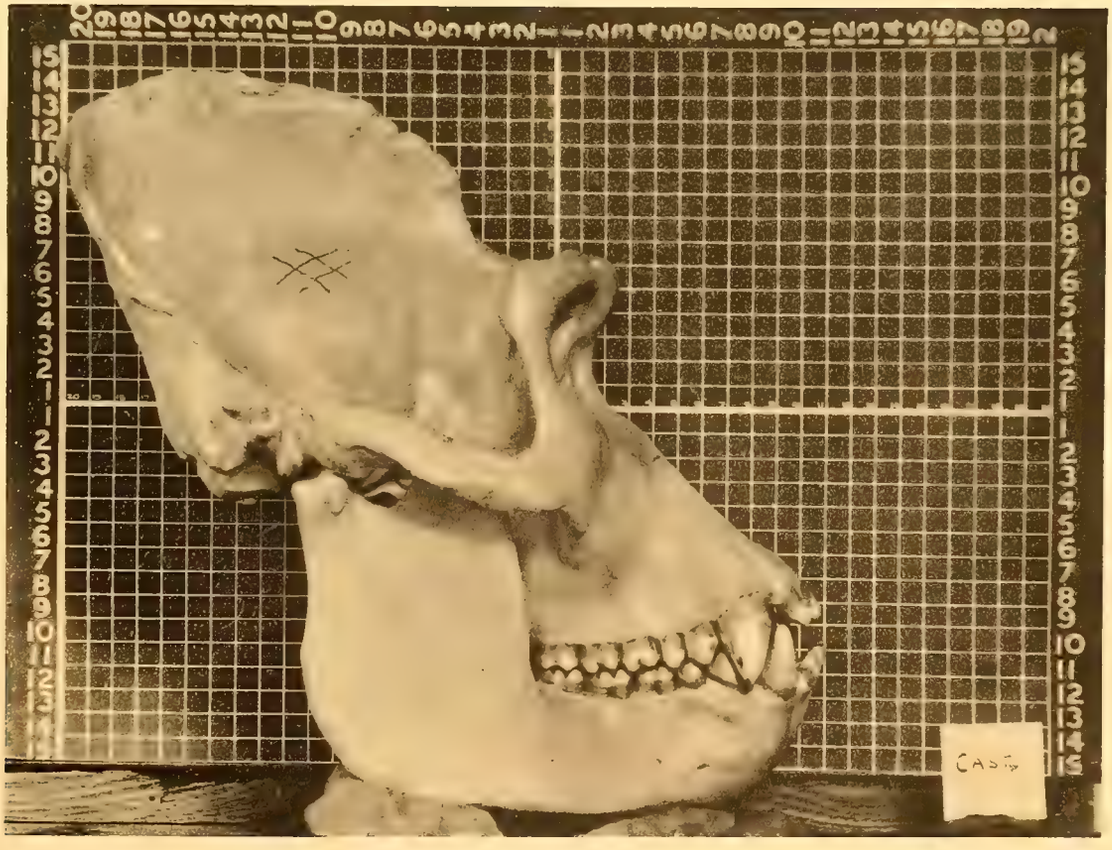


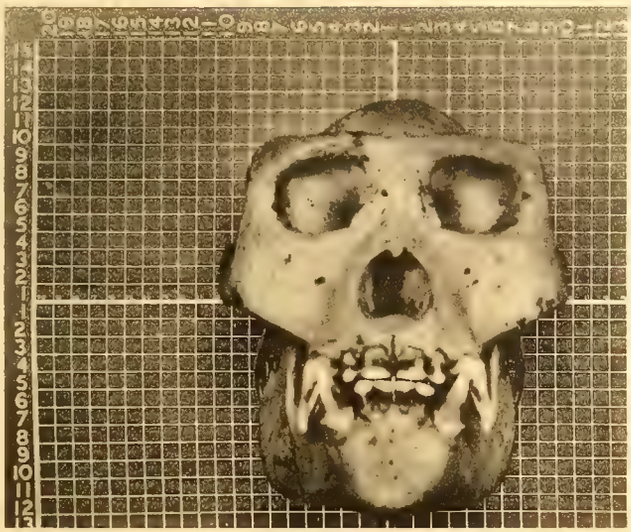
2

HELIOTYPE CO. BOSTON

PLATE 5.

PLATE 5.

Front, side, basal, and top views of a Cameroons gorilla skull in the Anatomisches Institute (Dr. Bolk collection), Amsterdam, Holland. This skull is just adult, a male without any crest, No. 1–1914. It shows an extreme variation.



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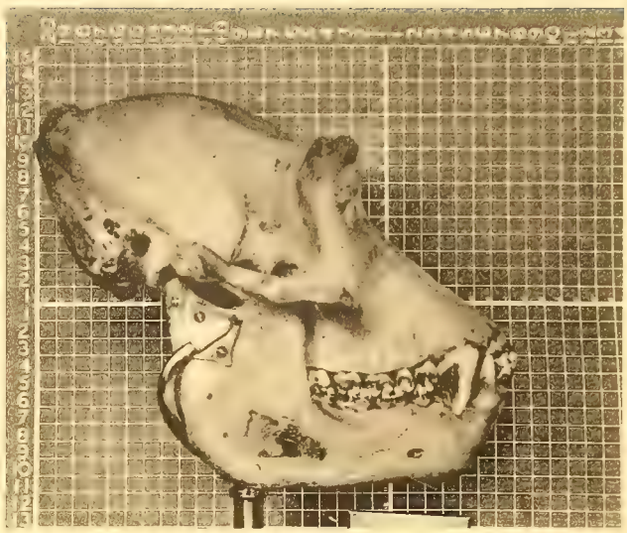

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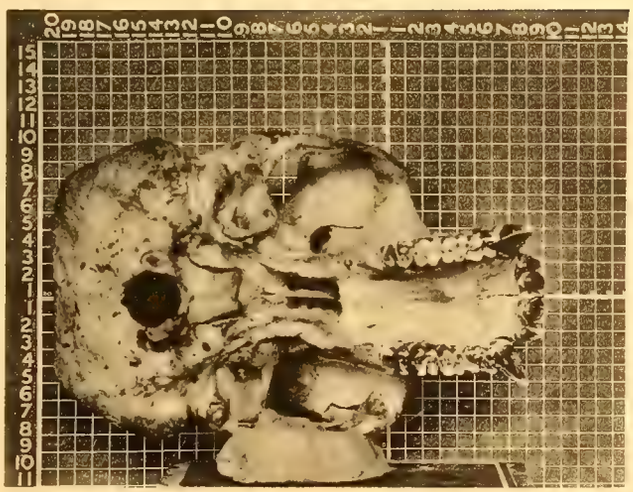

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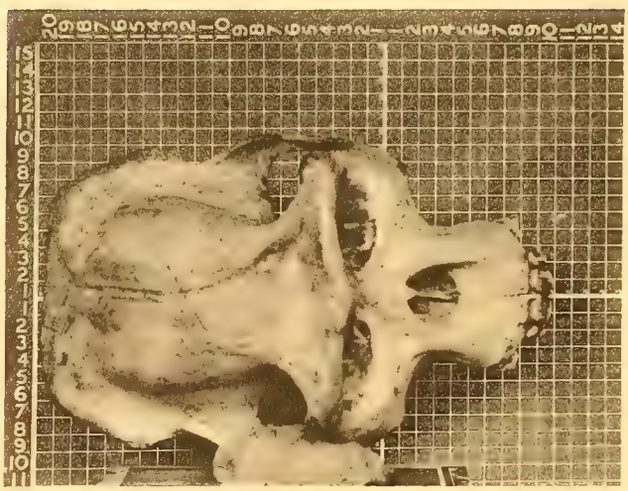


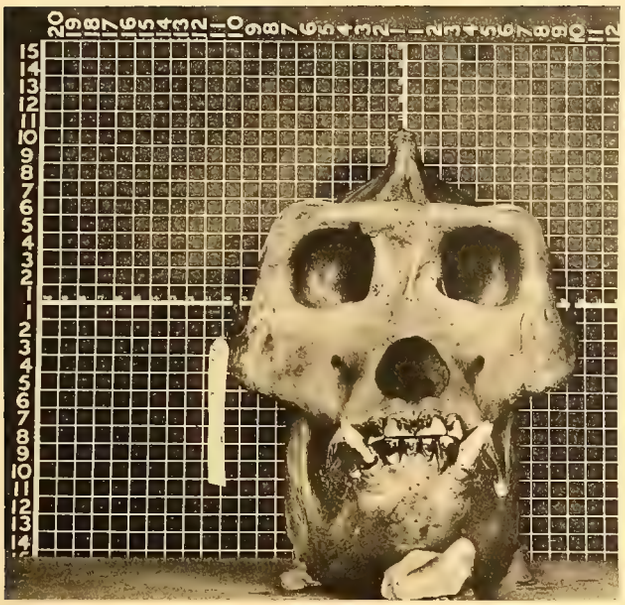
4

HELIOTYPE CO. BOSTON

PLATE 6.

PLATE 6.

Front, side, basal, and top views of a Gaboon gorilla skull from the region of Wesso in French Equatorial Africa. It is No. C.A. 503 in the Department of Comparative Anatomy of the American Museum of Natural History, New York. This skull is much less prognathous than the average. It shows an extreme of variation not unlike Figures 3 and 4 in Plate 2. Note also slight asymmetry.



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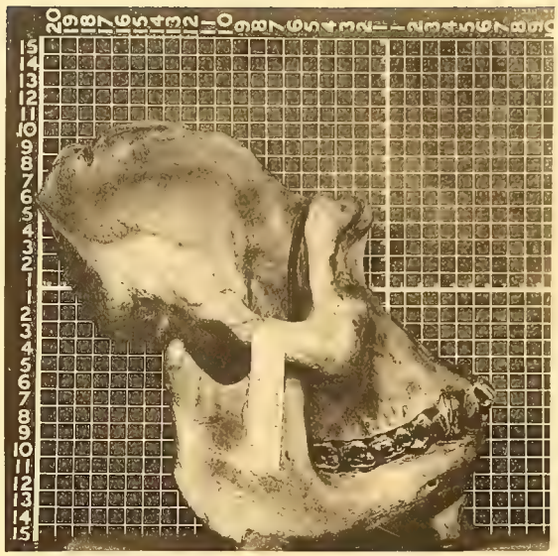

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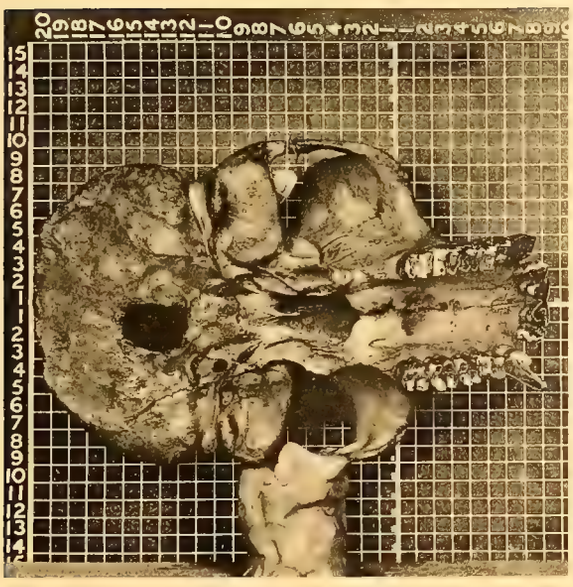

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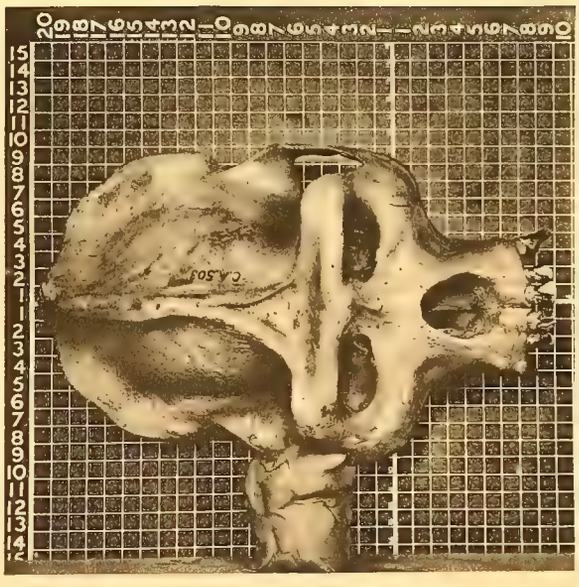


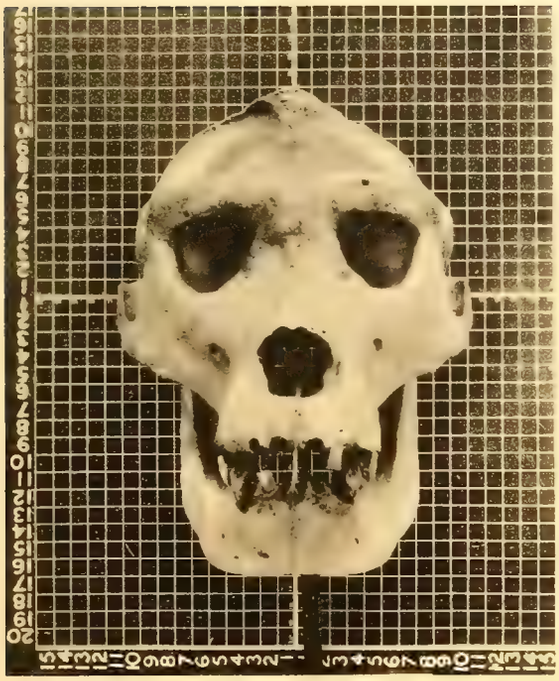
4

HELIOTYPE CO. BOSTON

PLATE 7.

PLATE 7.

Front and side views of two curious gorilla skulls. Above, No. 195, from Mubulu, French Congo, in Major Powell-Cotton's collection, Quex Park. Note great interorbital width. Below, No. G2, University Anatomy Institute, Oslo. Note length of face.



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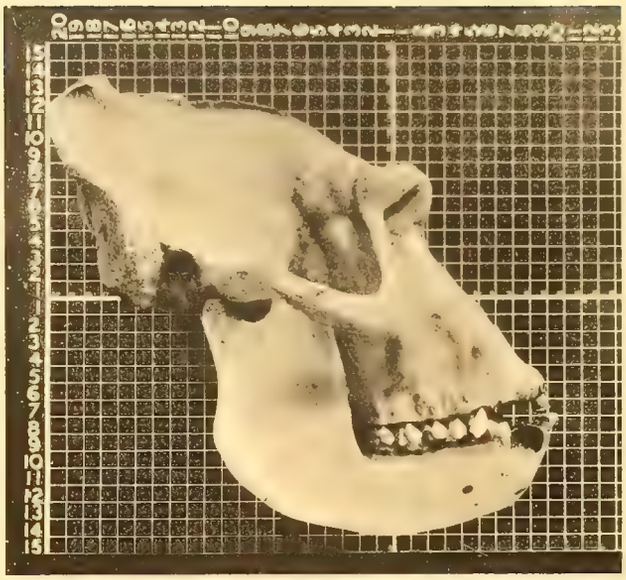

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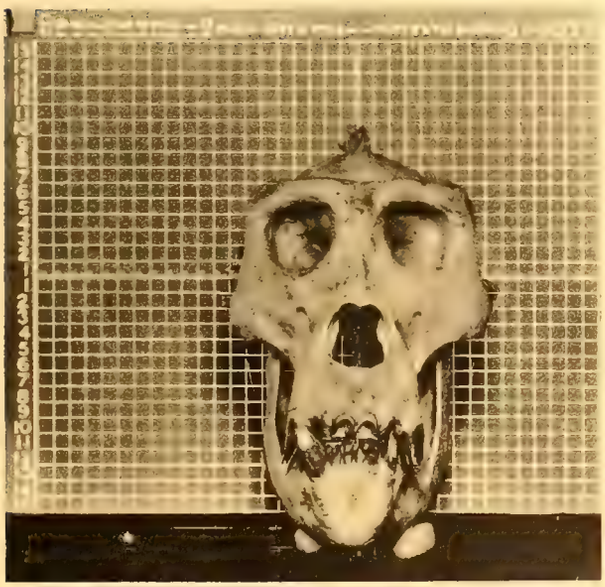

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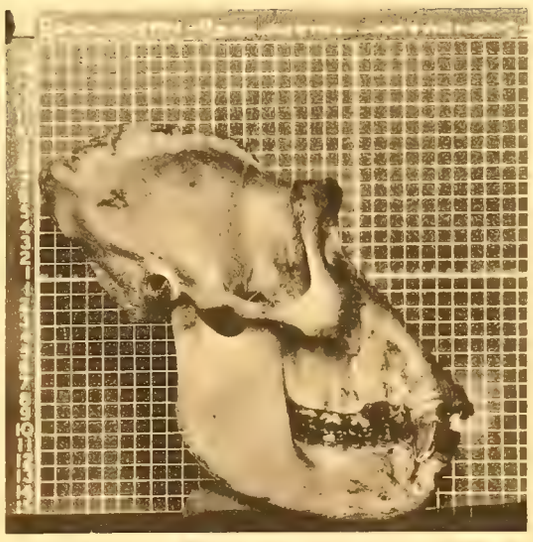


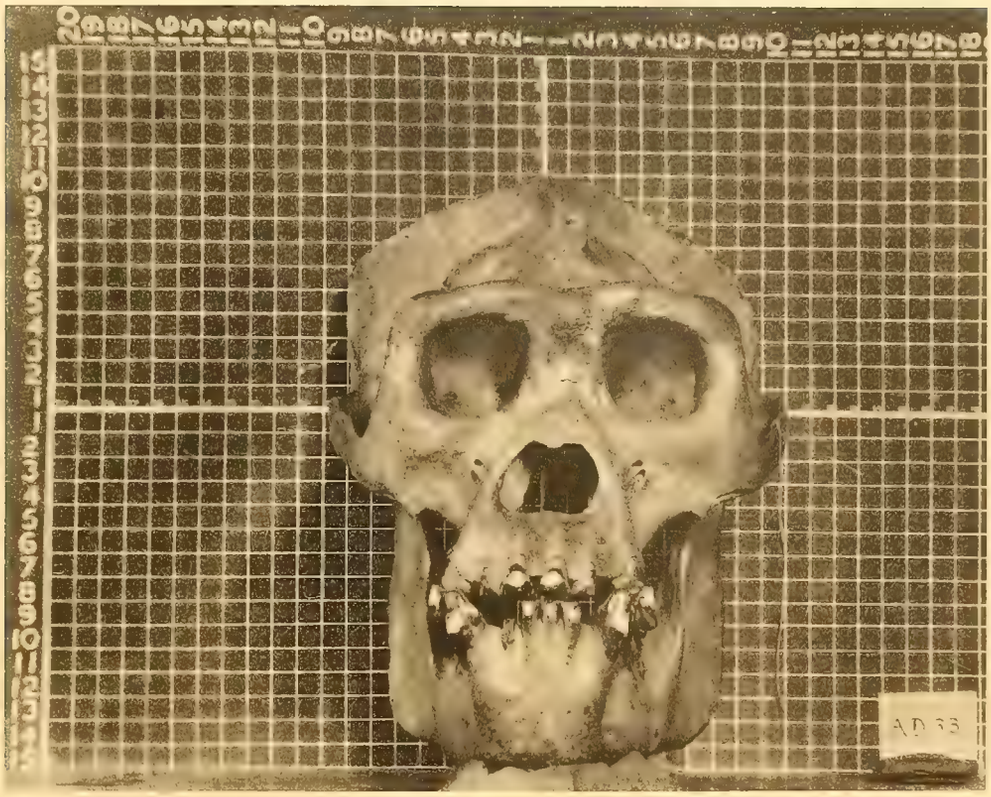
4

HELIOTYPE CO. BOSTON

PLATE 8.

PLATE 8.

Front and basal views of Kivu Volcano gorilla in Lord Rothschild's collection at Tring, England, No. A.D. 33. Note especially marked asymmetry.



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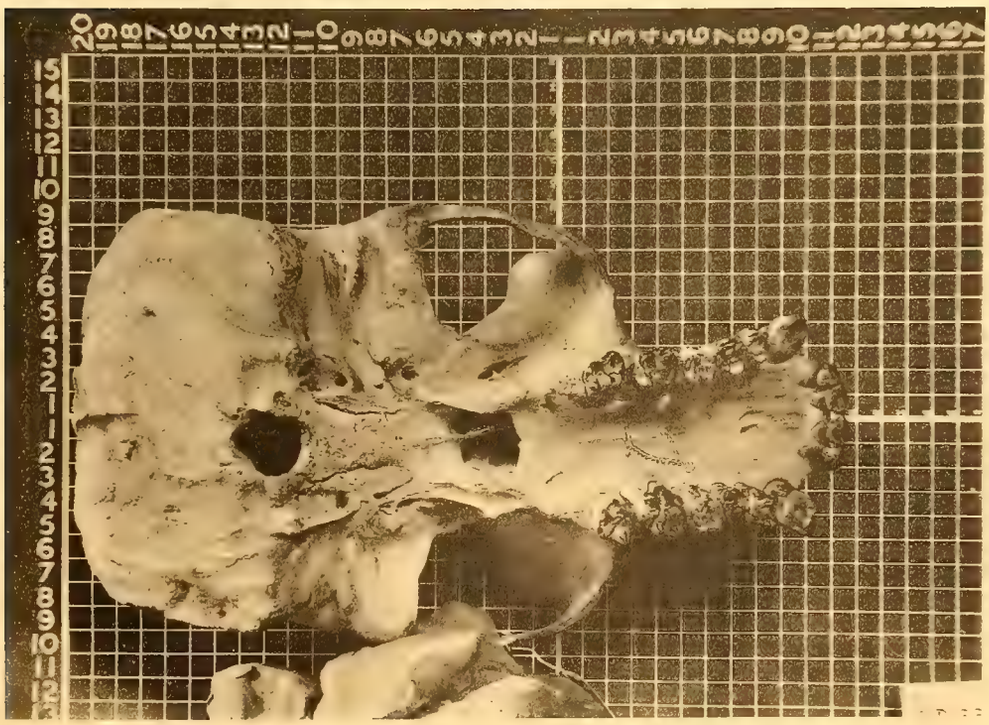


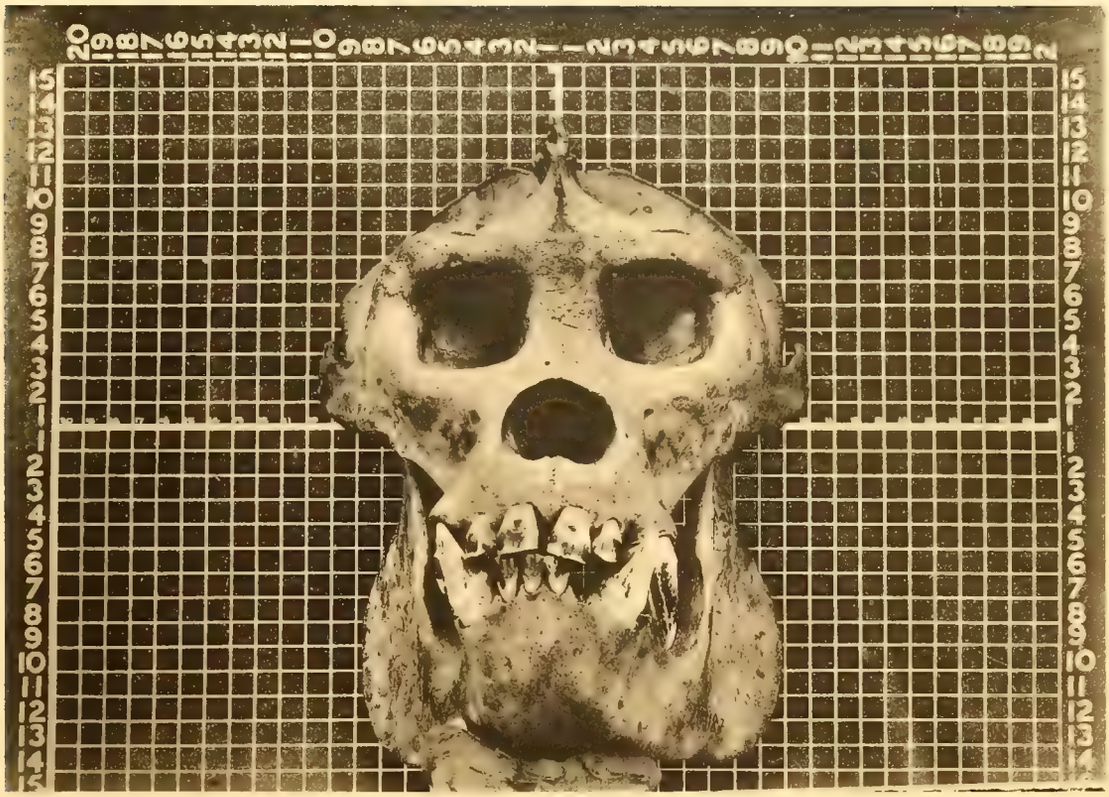
2

HELIOTYPE CO. BOSTON

PLATE 9.

PLATE 9.

Front and basal views of eastern Mountain Gorilla from Luofu, No. R.G. 8187, Congo Museum, Tervueren, Belgium. Compare this with Plate 8.



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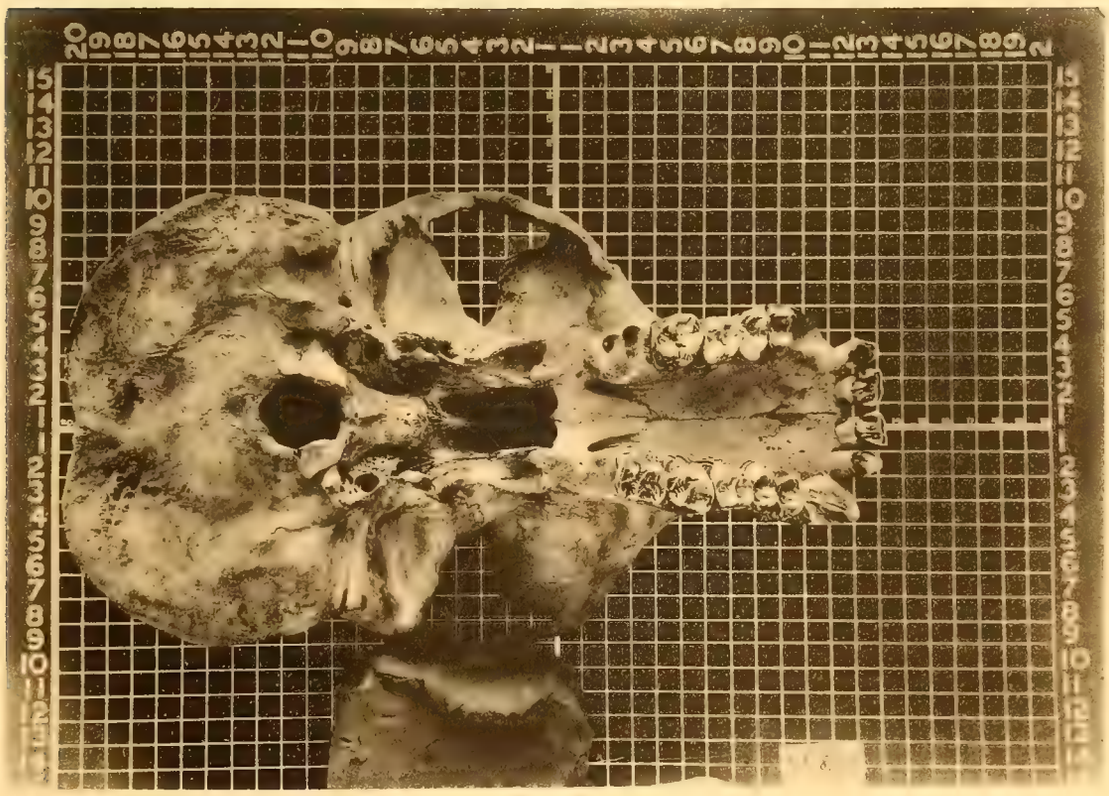


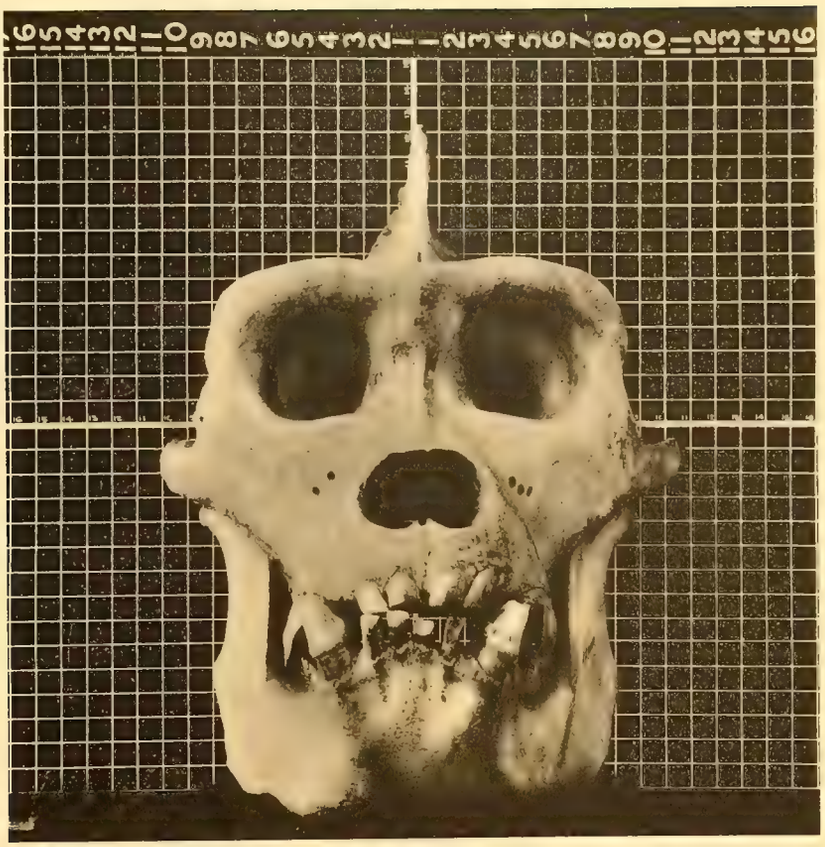
2

HELIOTYPE CO. BOSTON

PLATE 10.

PLATE 10.

Side and front views of large Cameroons gorilla, No. 17960, Berlin Museum (type of Matschie's *Gorilla hansmeyeri*).



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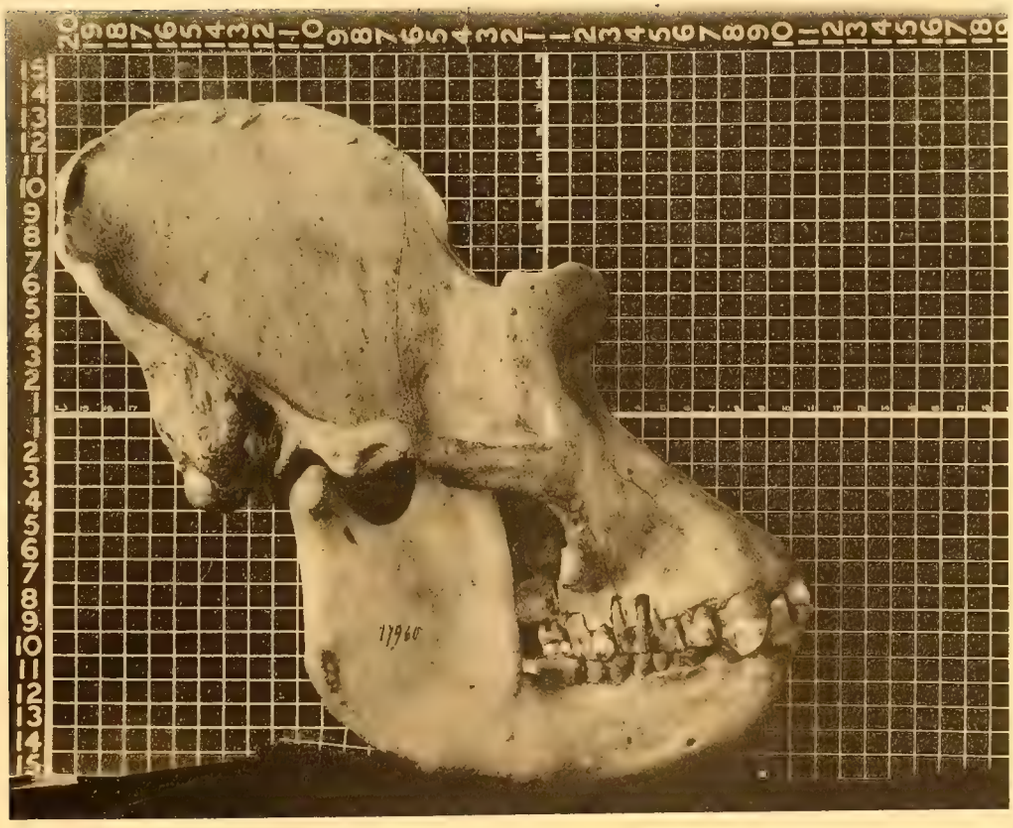
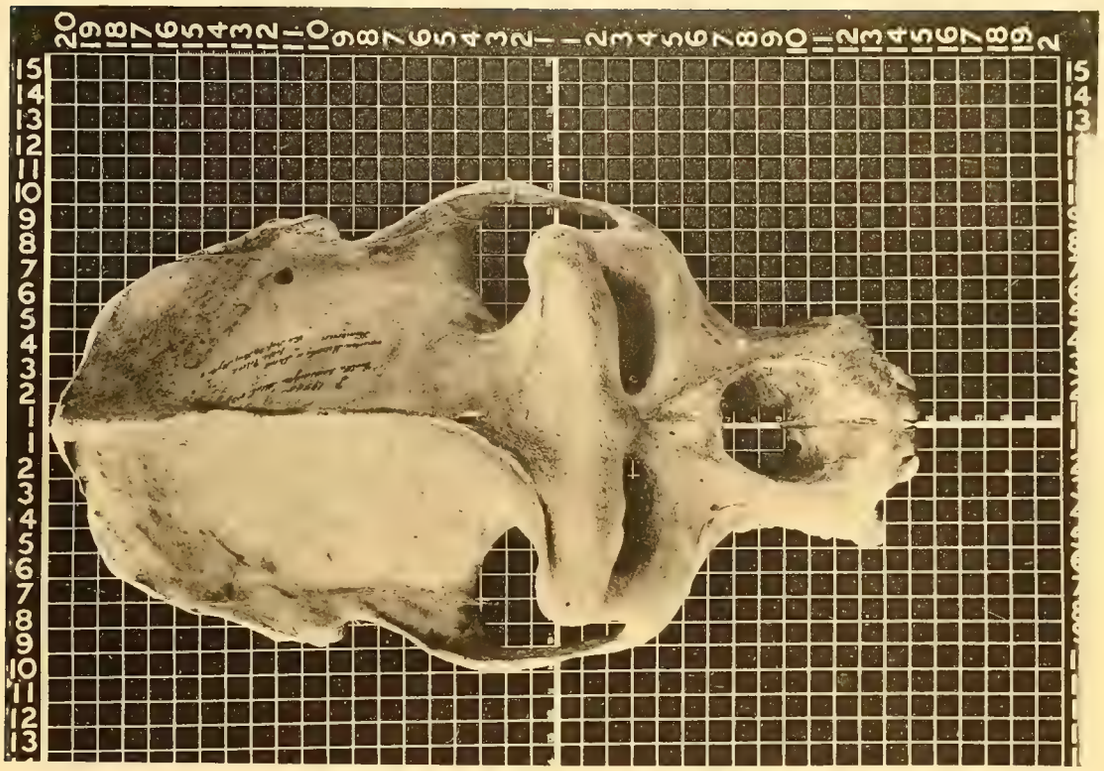


2

PLATE 11.

PLATE 11.

Top and basal views of large Cameroons gorilla, No. 17960, Berlin Museum (type of Matschie's *Gorilla hansmeyeri*).



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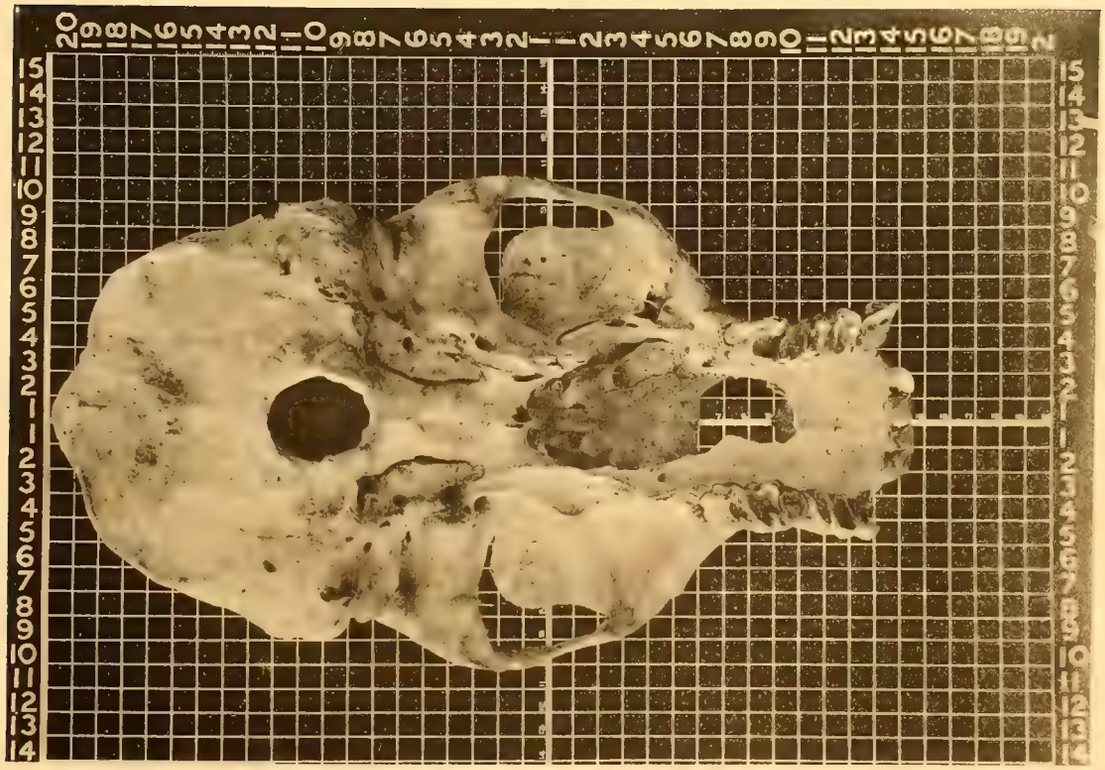


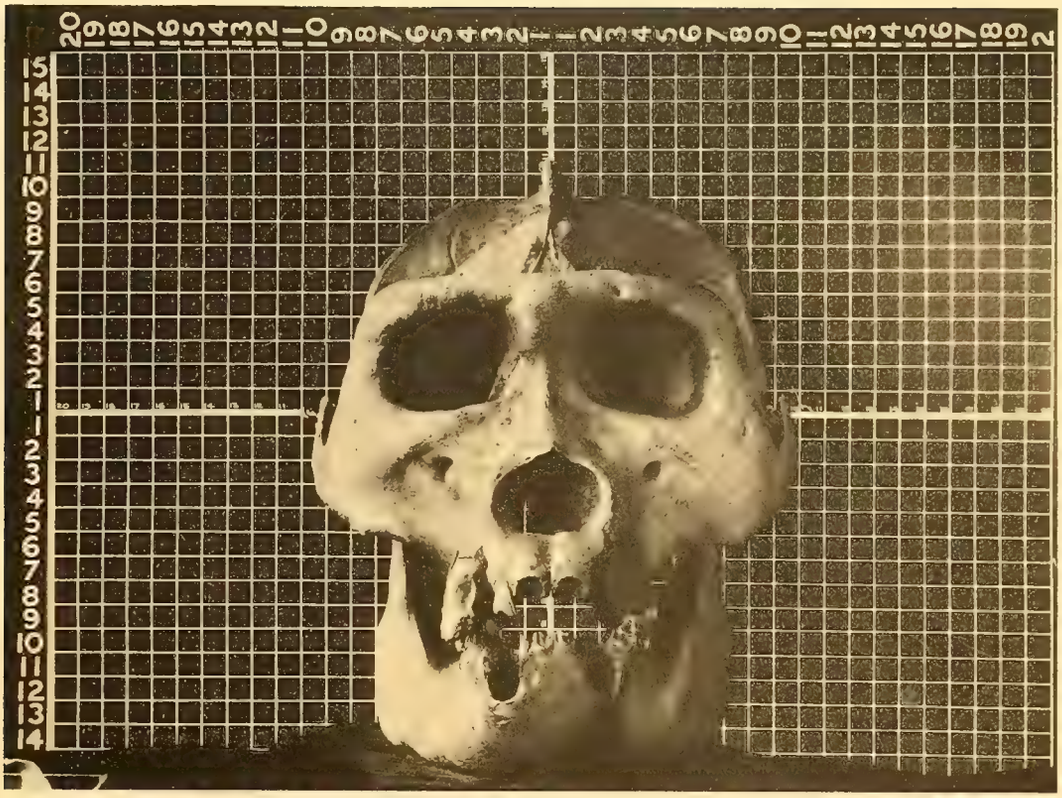
2

HELIOTYPE CO. BOSTON

PLATE 12.

PLATE 12.

Side and front views of Western Cameroons gorilla, No. 12789, Berlin Museum (type of Matschie's *Gorilla diehli*).



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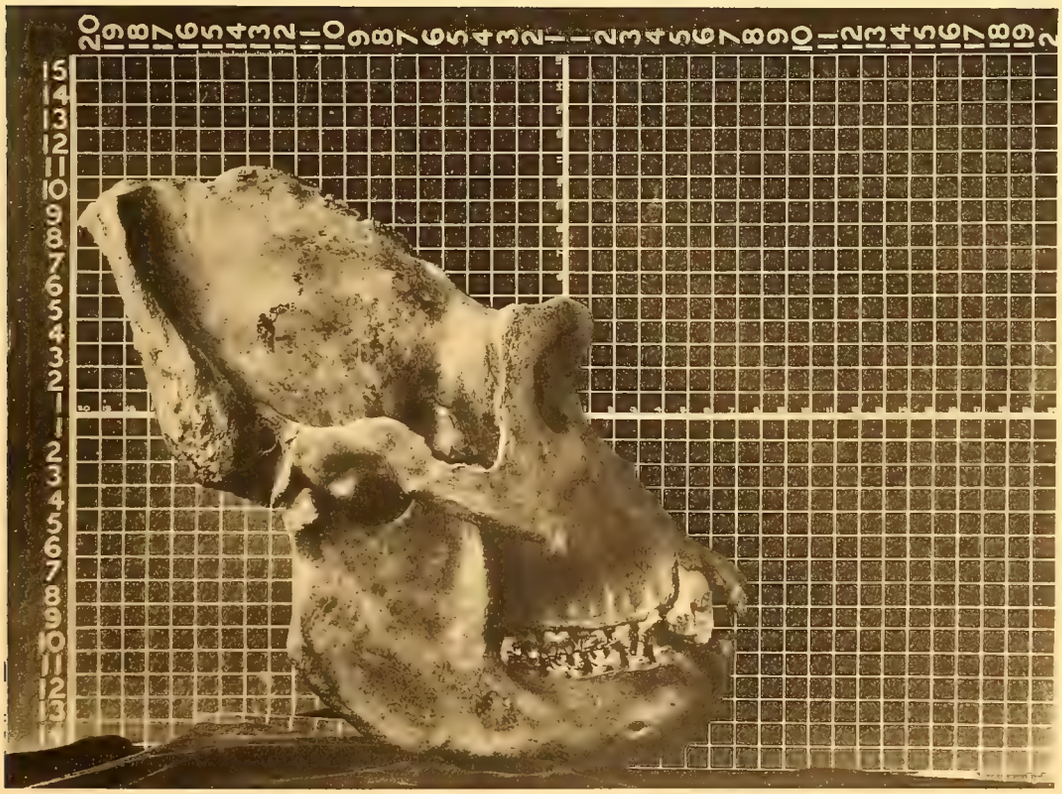


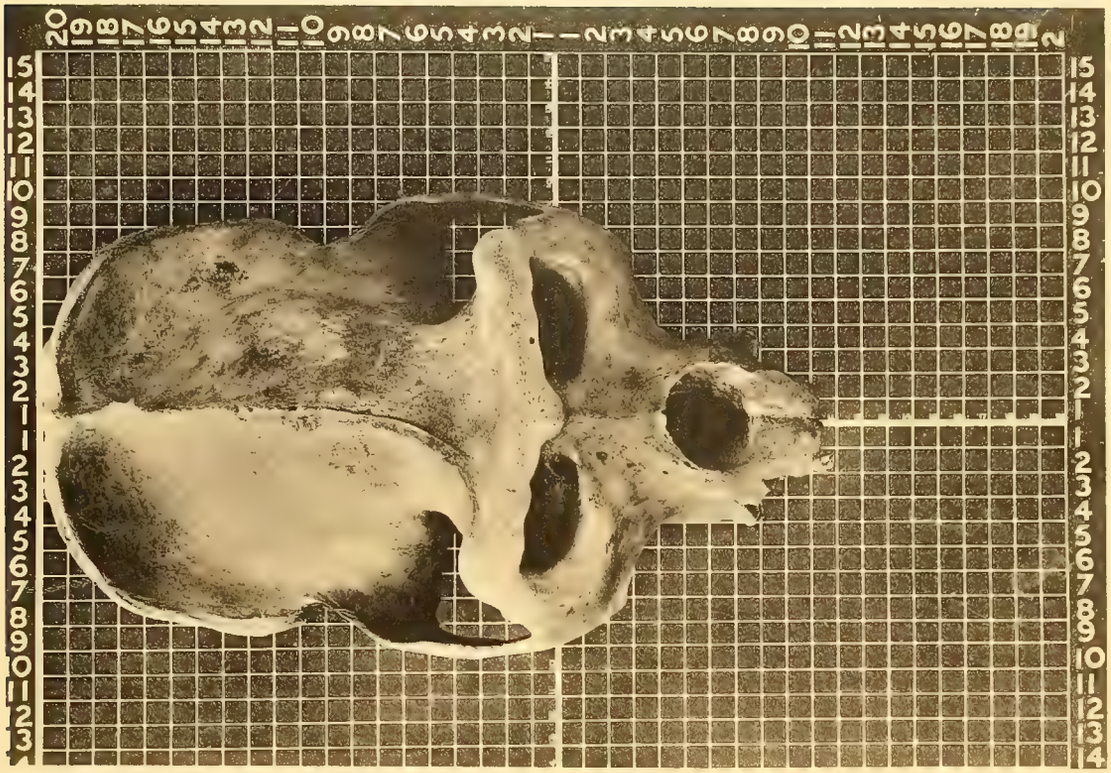
2

HELIOTYPE CO. BOSTON

PLATE 13.

PLATE 13.

Top and basal views of Western Cameroons gorilla, No. 12789, Berlin Museum (type of Matschie's *Gorilla diehli*).



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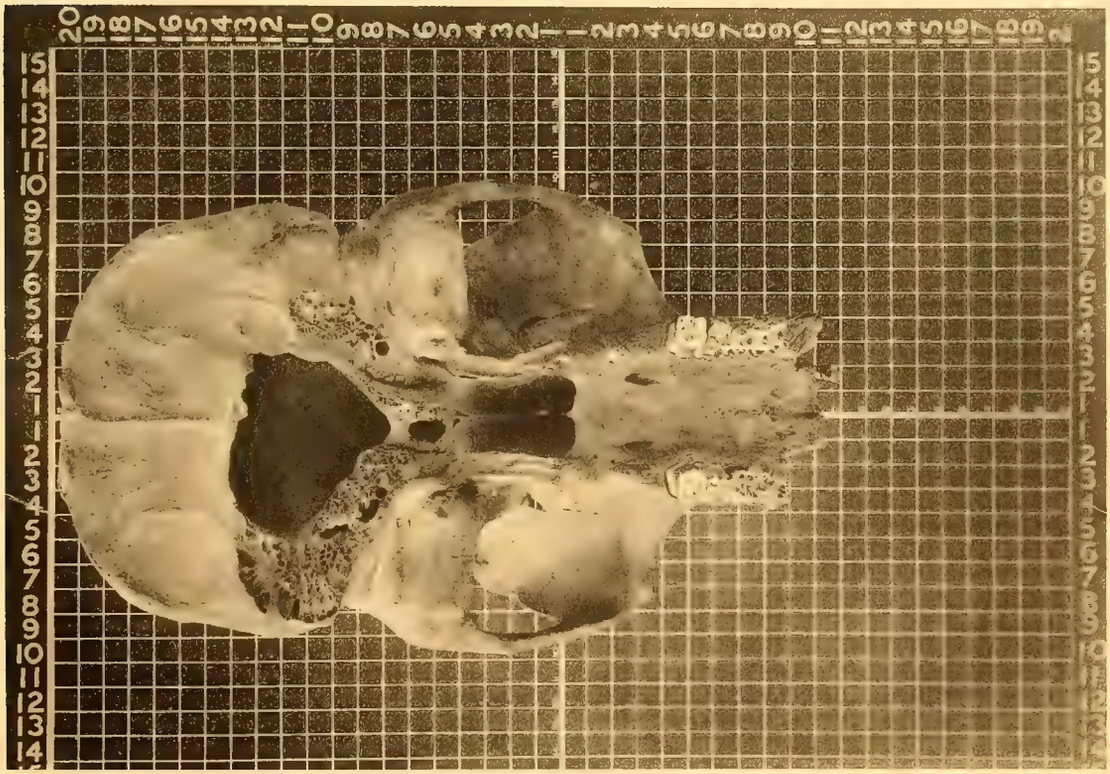


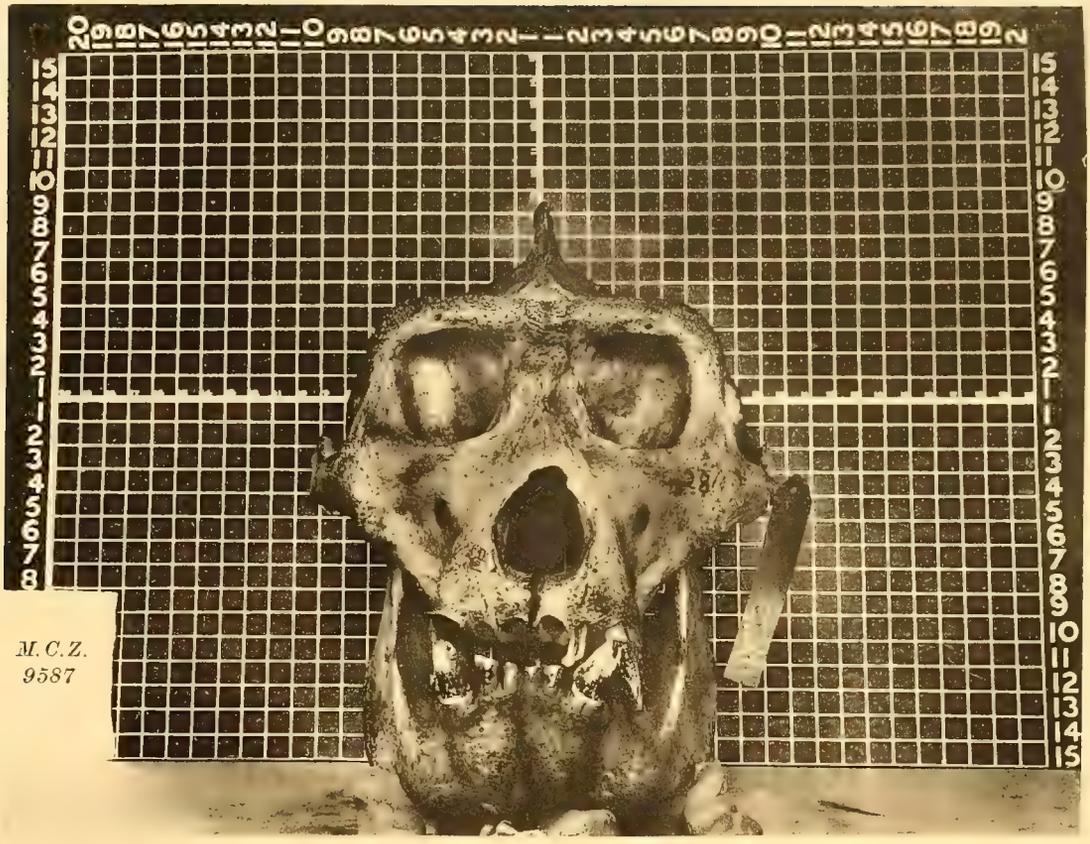
2

HELIOTYPE CO. BOSTON

PLATE 14.

PLATE 14.

Side and front views of a Gaboon skull. An original cotype of *Gorilla gorilla* (Savage and Wyman), No. 9587, male, collection of the Museum of Comparative Zoölogy.



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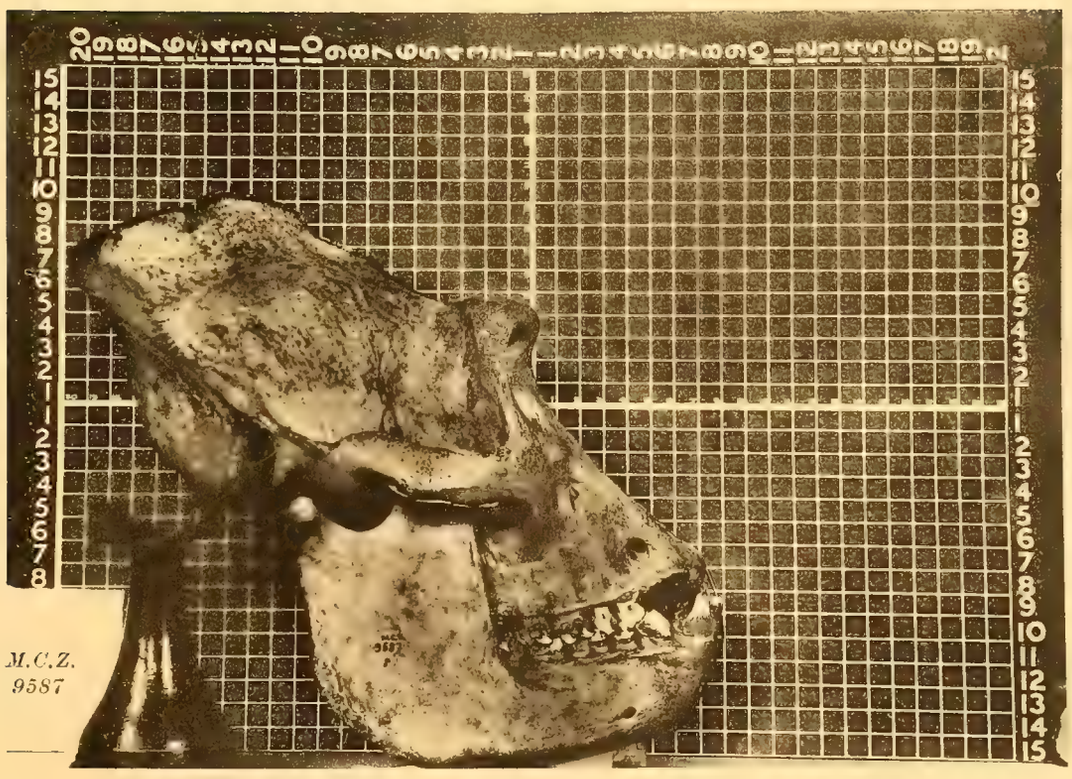


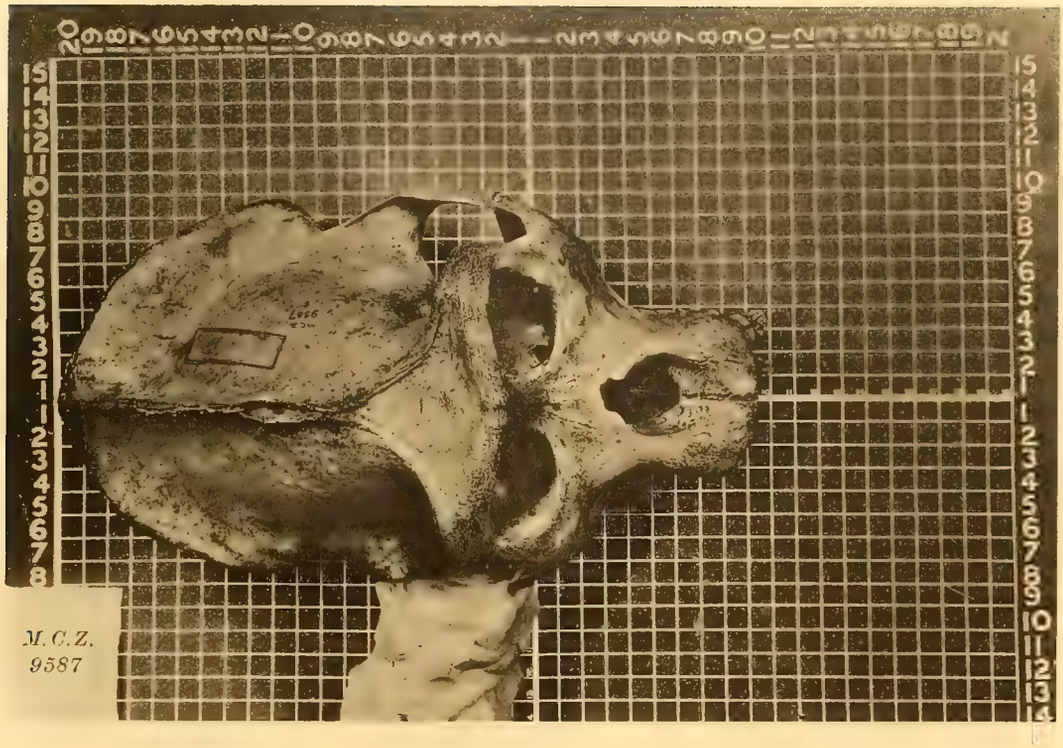
2

HELIOTYPE CO. BOSTON

PLATE 15.

PLATE 15.

Top and basal views of a Gaboon skull. An original cotype of *Gorilla gorilla* (Savage and Wyman), No. 9587, male, collection of the Museum of Comparative Zoölogy.



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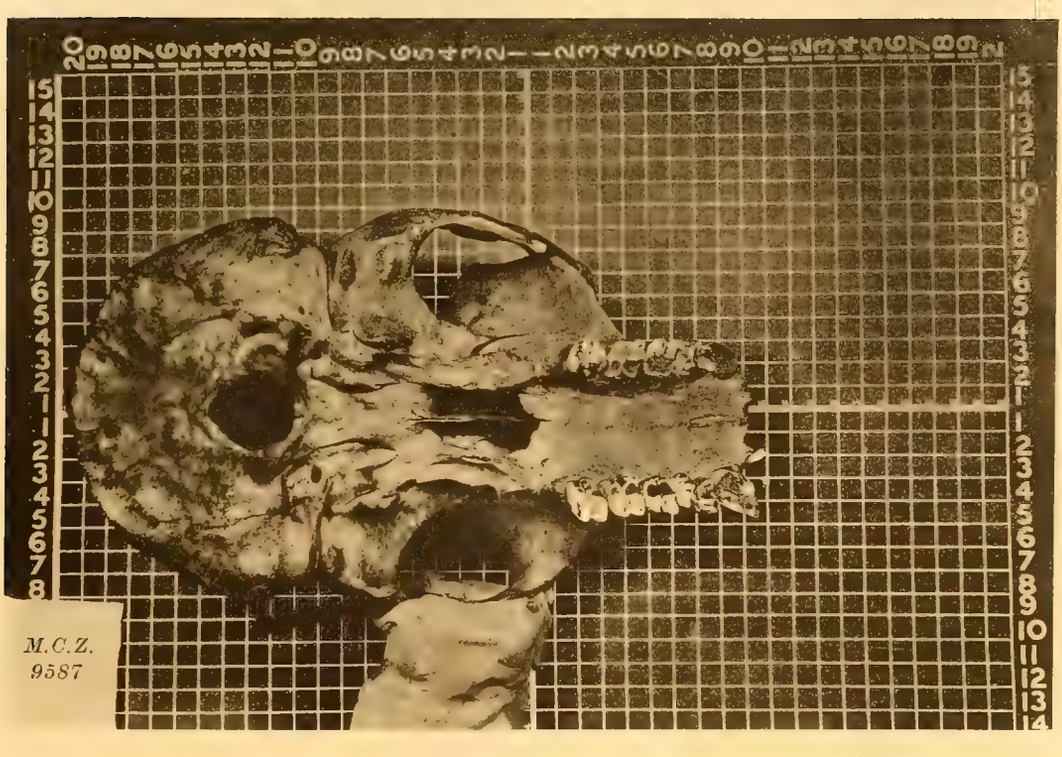


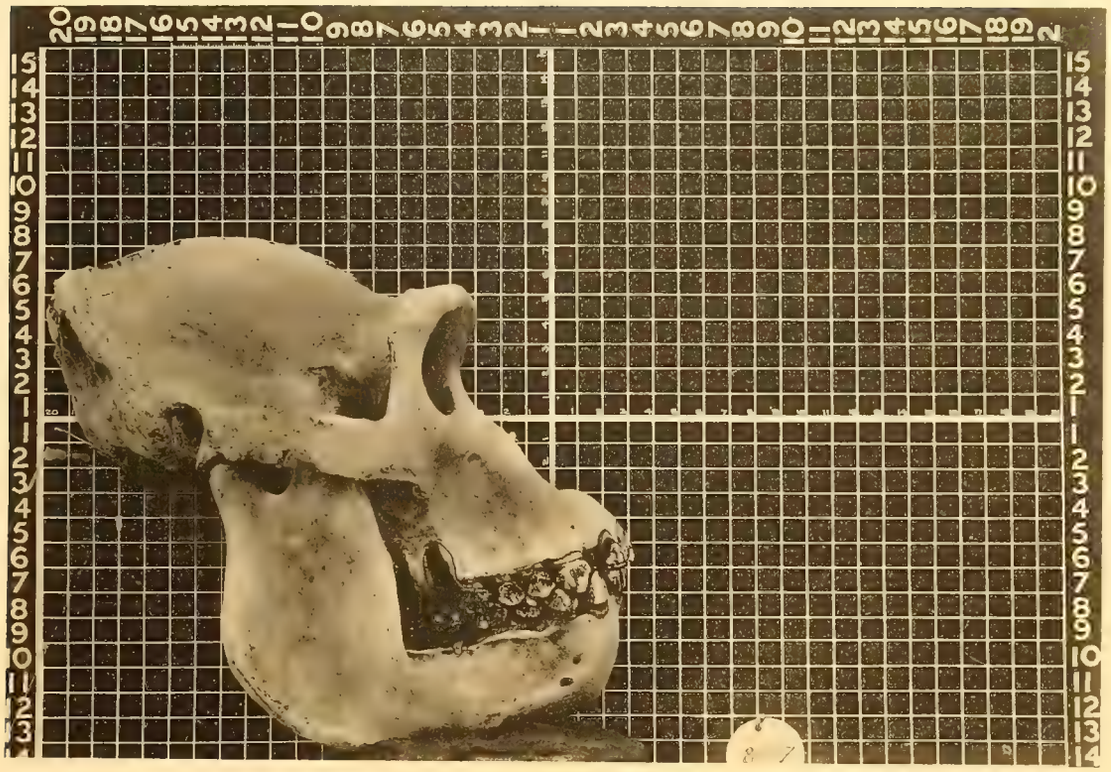
2

HELIOTYPE CO. BOSTON

PLATE 16.

PLATE 16.

Side view of male (lower) and female (upper) Mountain Gorilla skulls from Kivu Volcanoes, Nos. R.G. 2257 and 8607, Congo Museum, Tervueren.



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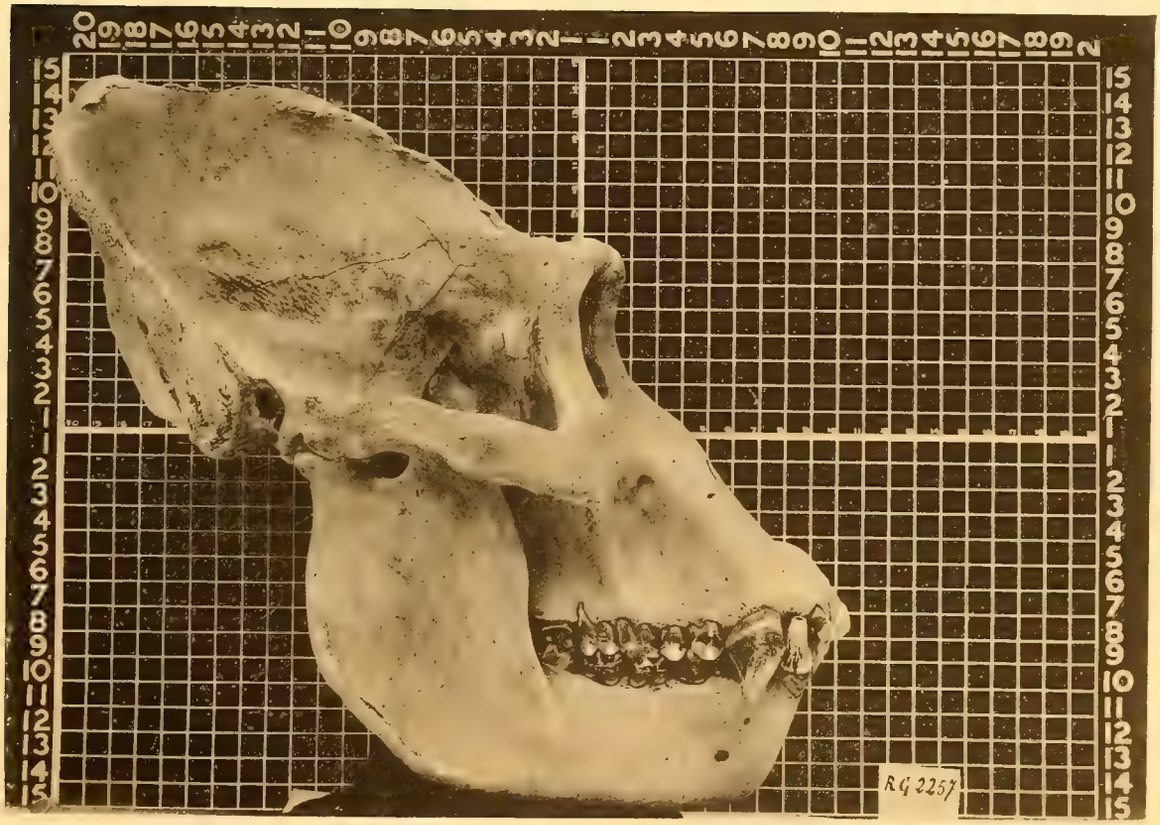


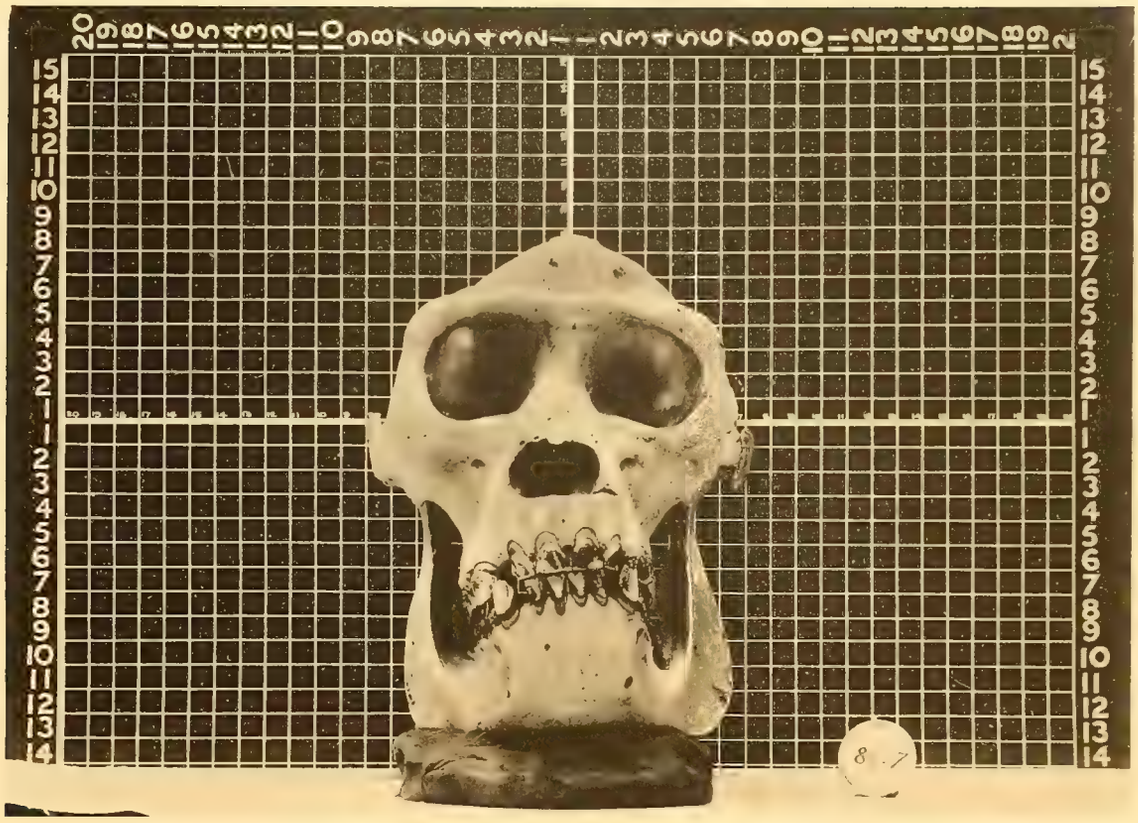
2

HELIOTYPE CO. BOSTON

PLATE 17.

PLATE 17.

Front views of male (below) and female (above) Mountain Gorilla skulls from Kivu Volcanoes, Nos. R.G. 2257 and 8607, Congo Museum, Tervueren.



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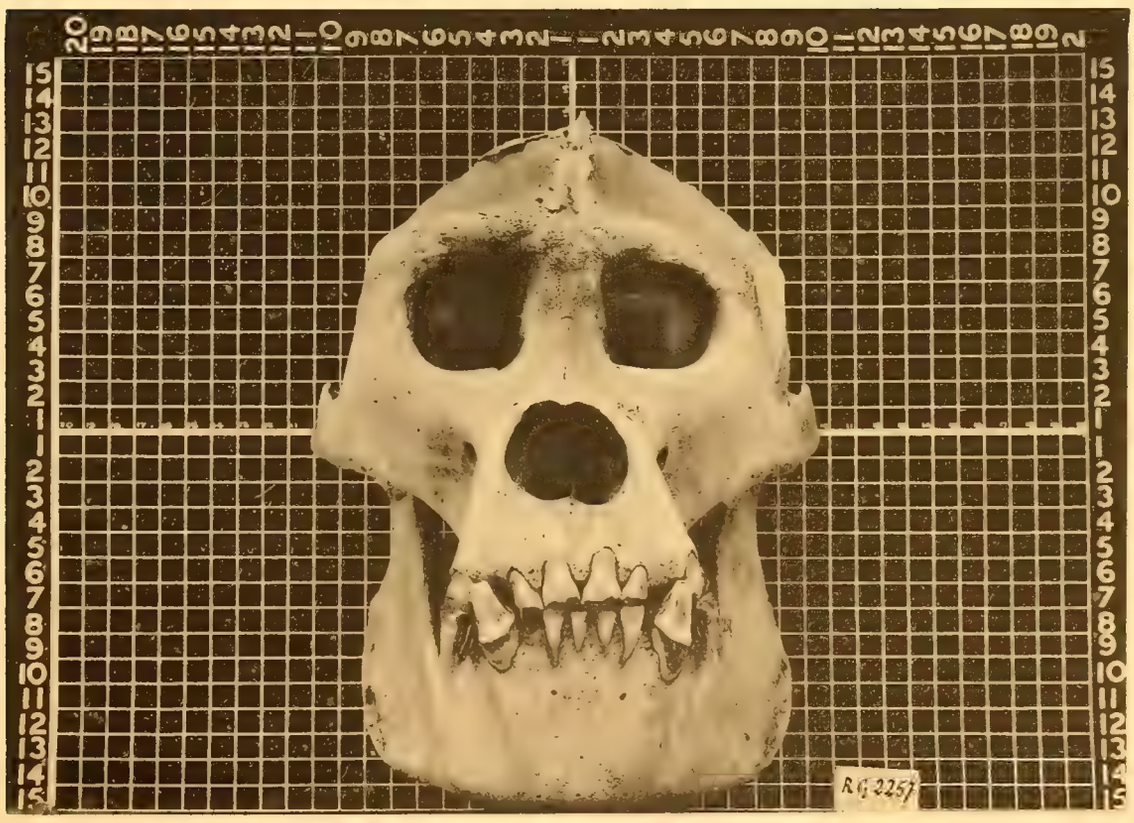


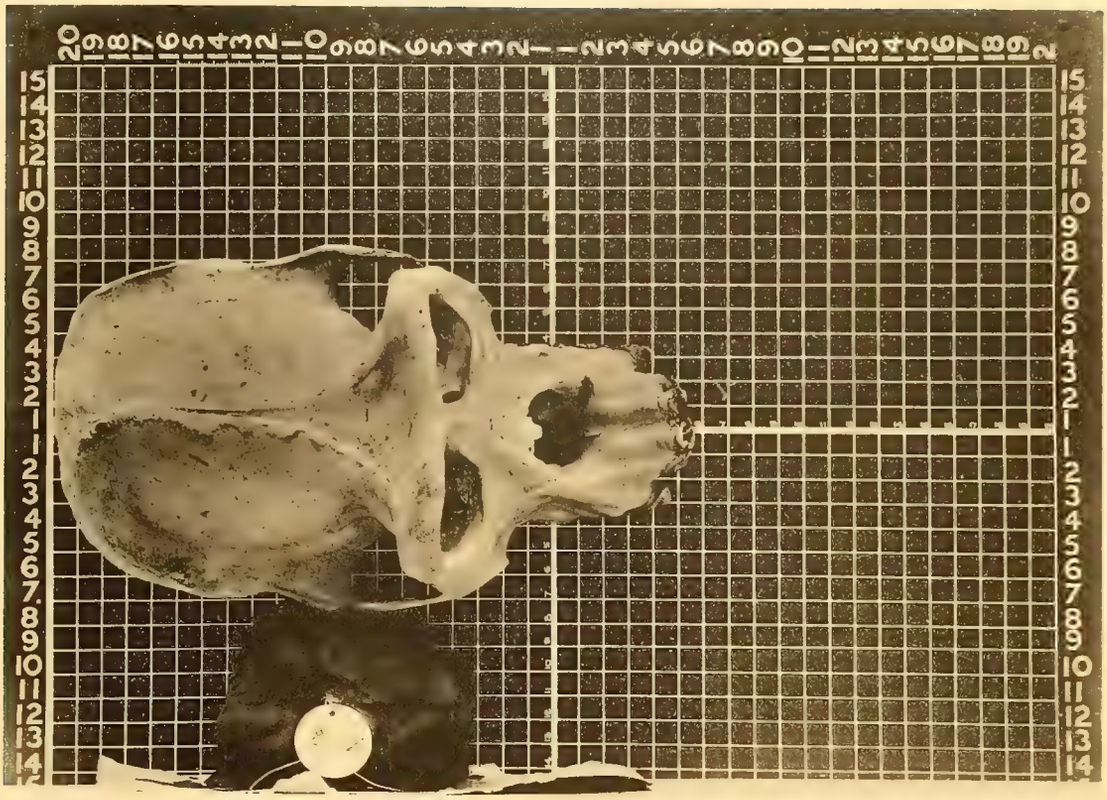
2

HELIOTYPE CO. BOSTON

PLATE 18.

PLATE 18.

Top views of male (below) and female (above) Mountain Gorilla skulls from Kivu Volcanoes, Nos. R.G. 2257 and 8607, Congo Museum, Tervueren. Note asymmetry in female skull.



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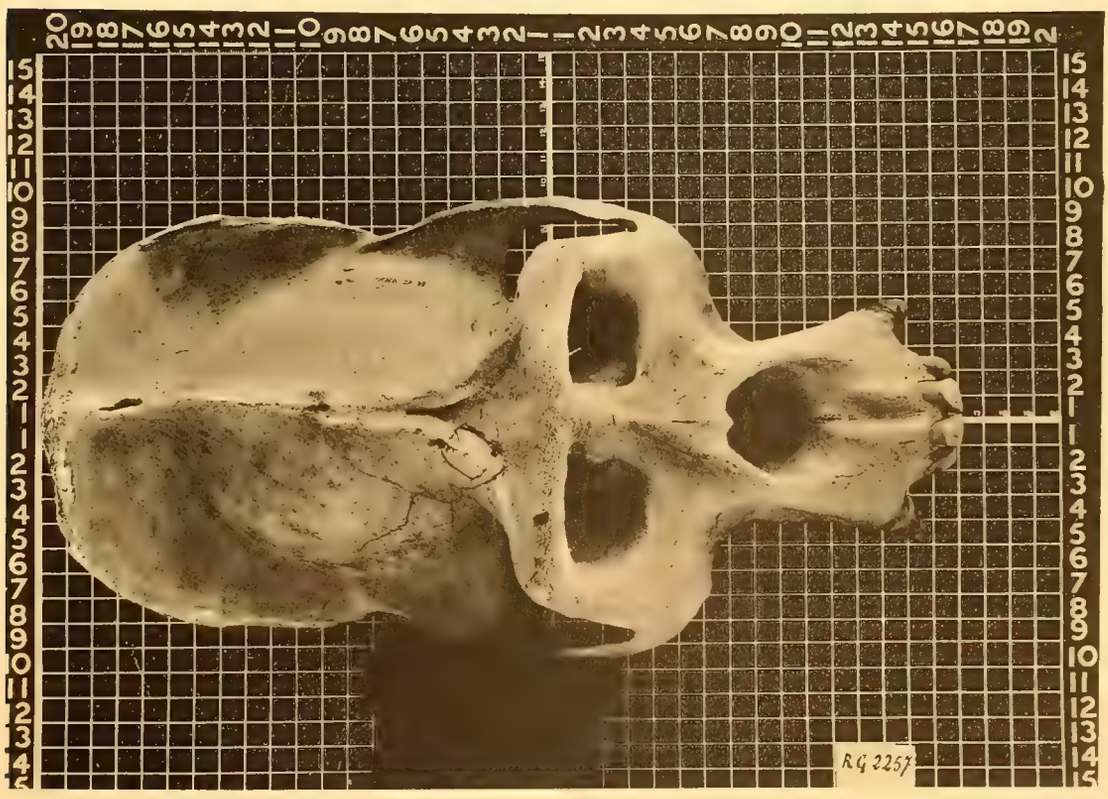
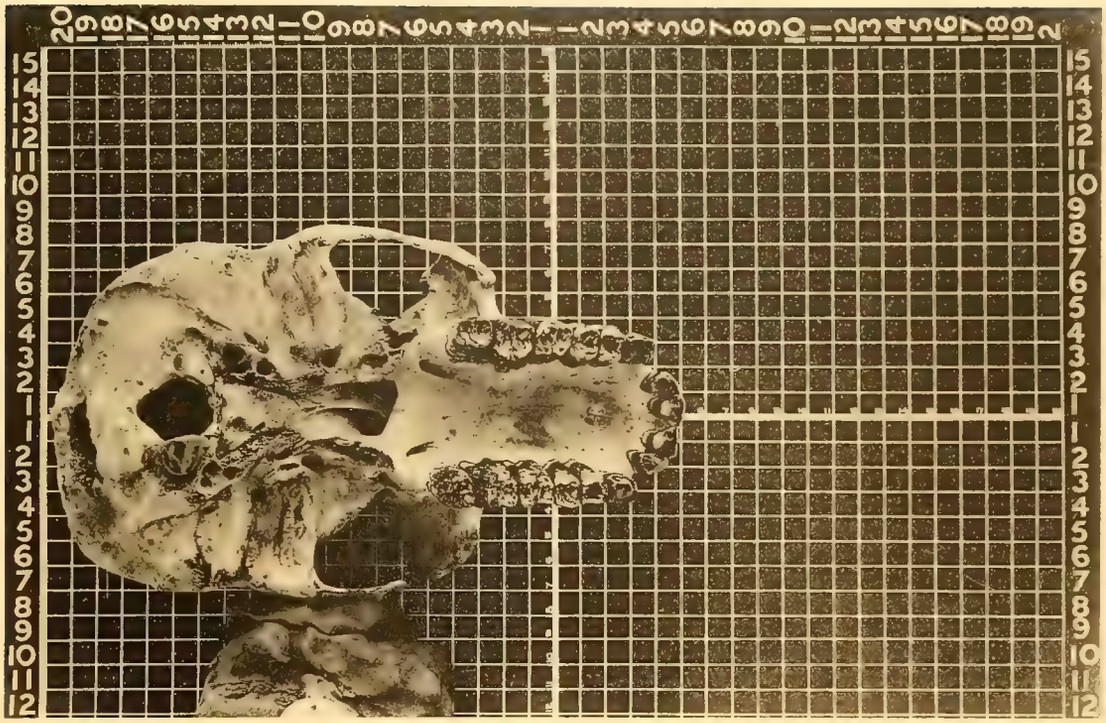


2

PLATE 19.

PLATE 19.

Basal views of male (below) and female (above) Mountain Gorilla skulls, from Kivu Volcanoes, Nos. R.G. 2257 and 8607, Congo Museum, Tervueren. Note asymmetry in female skull.



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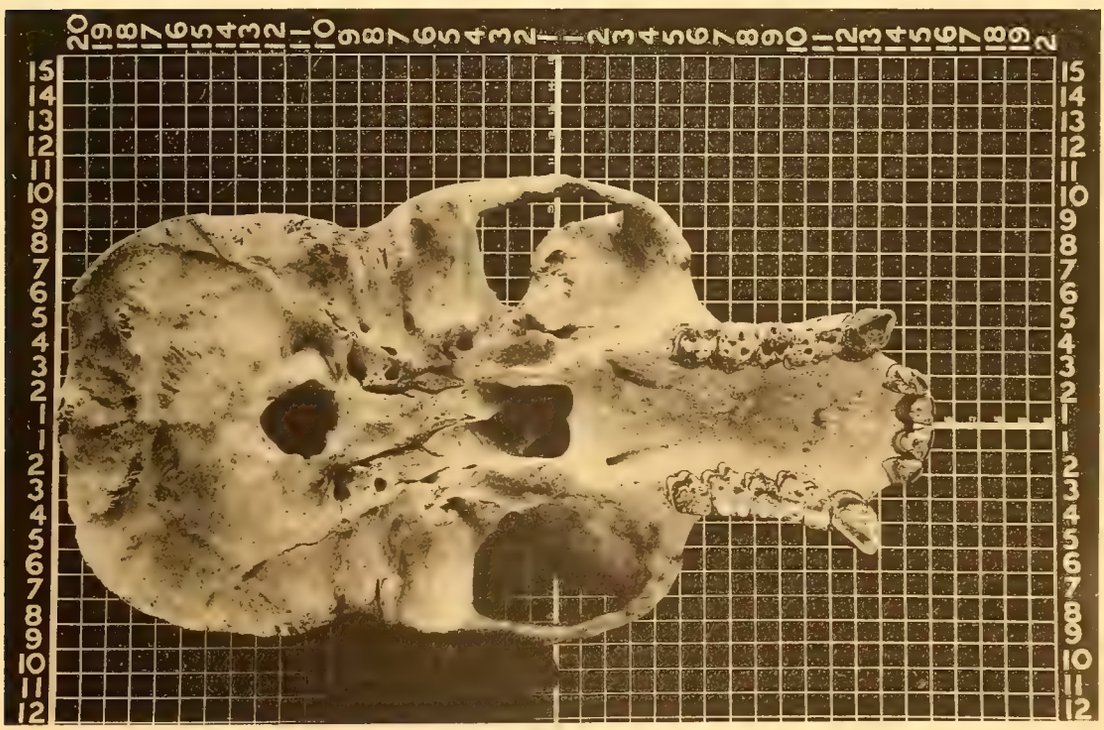


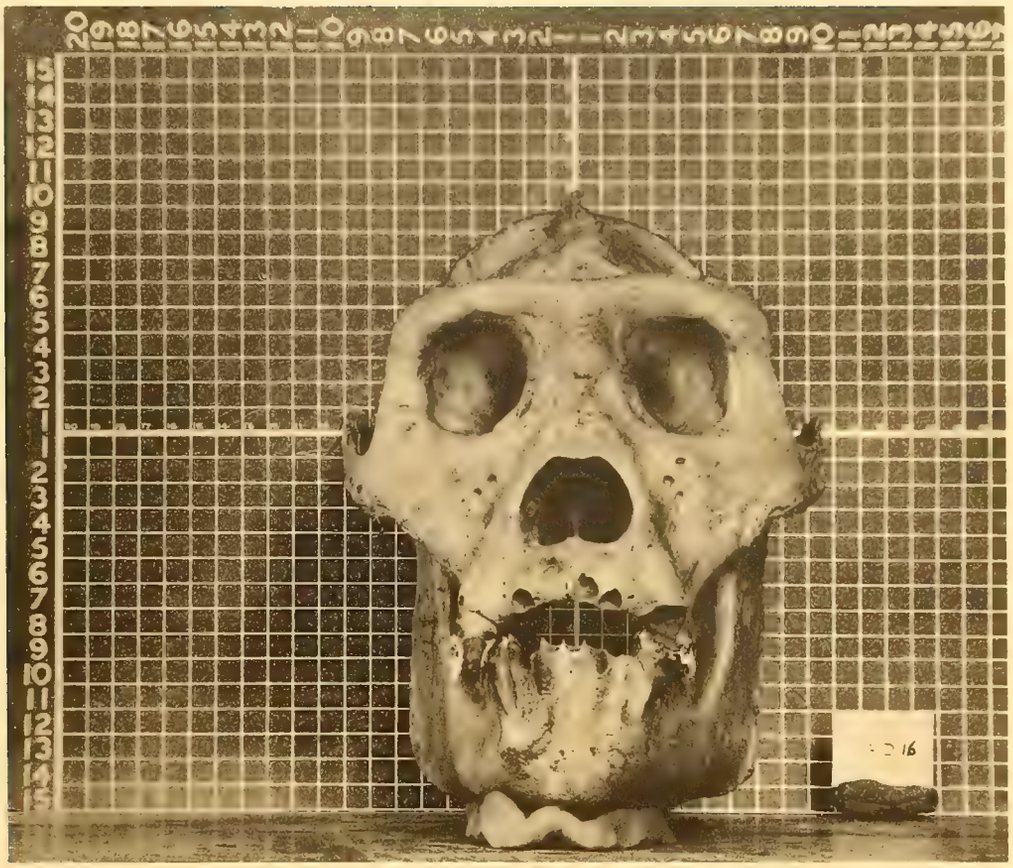
2

HELIOTYPE CO. BOSTON

PLATE 20.

PLATE 20.

Front and side views of skull from Brazenor, upper French Congo. No. A.D. 16, Lord Rothschild's collection at Tring, England. This skull comes closest to the average in general measurements for the entire genus Gorilla of any that I have photographs of.



1

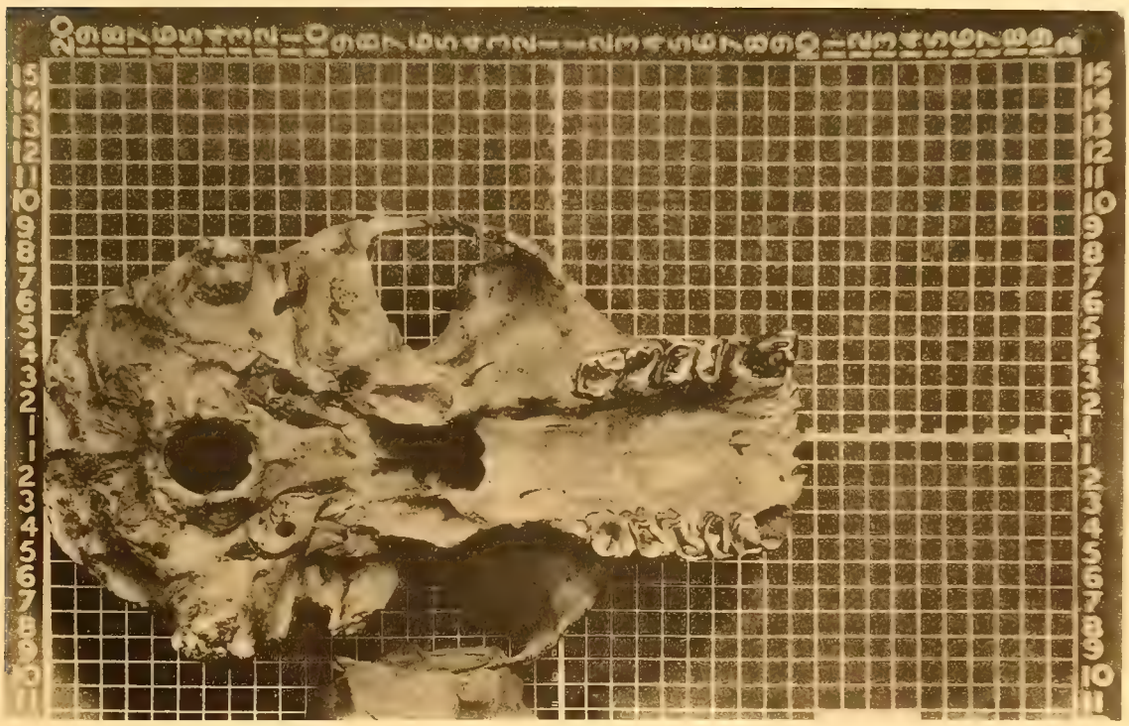
2

PLATE 21.

PLATE 21.

Top and basal views of skull from Brazenor, upper French Congo, No. A.D. 16, Lord Rothschild's collection at Tring, England. This skull comes closest to the average in general measurements for the entire genus Gorilla of any that I have photographs of.

1



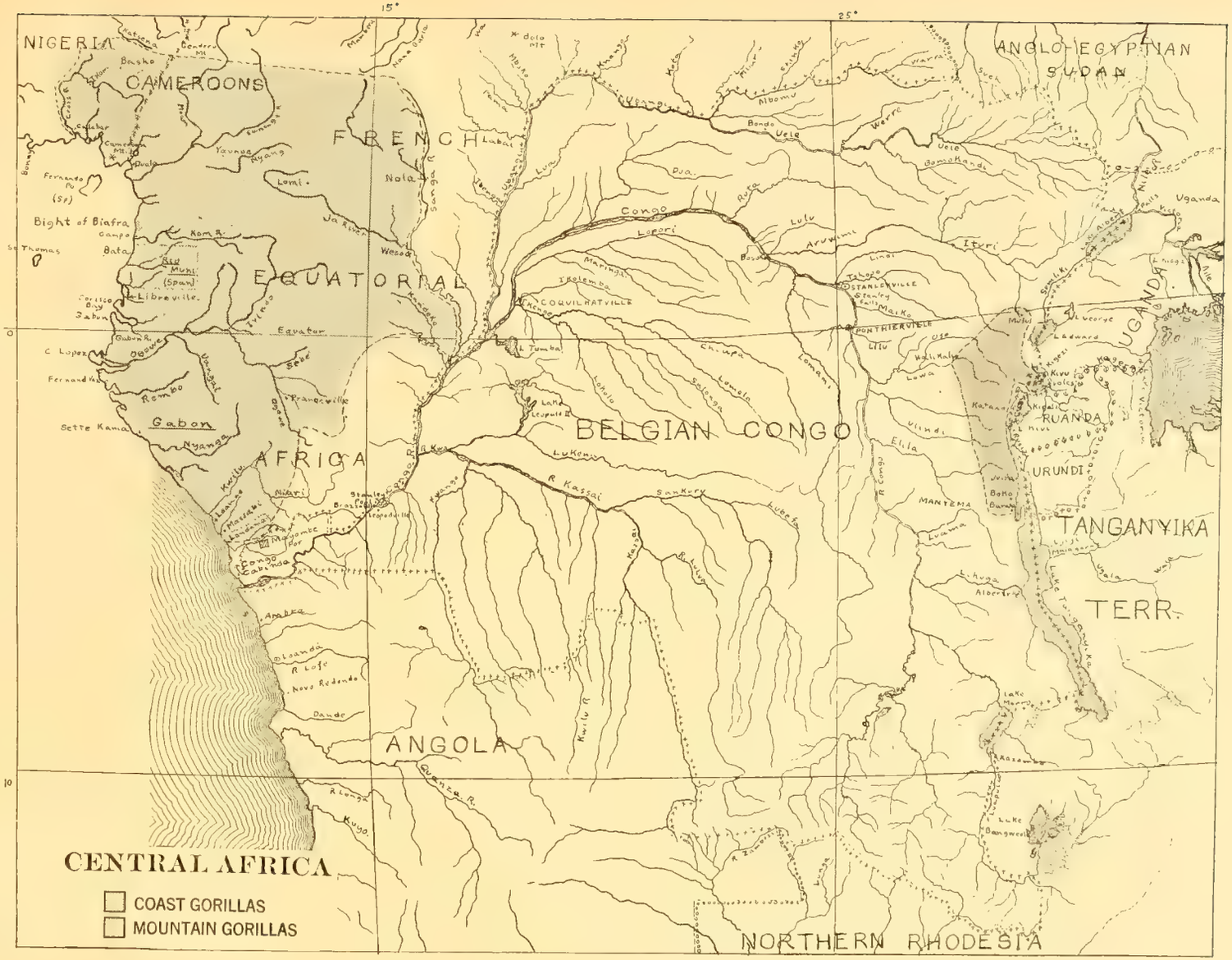
2

HELIOTYPE CO. BOSTON

MAP 1.

MAP 1.

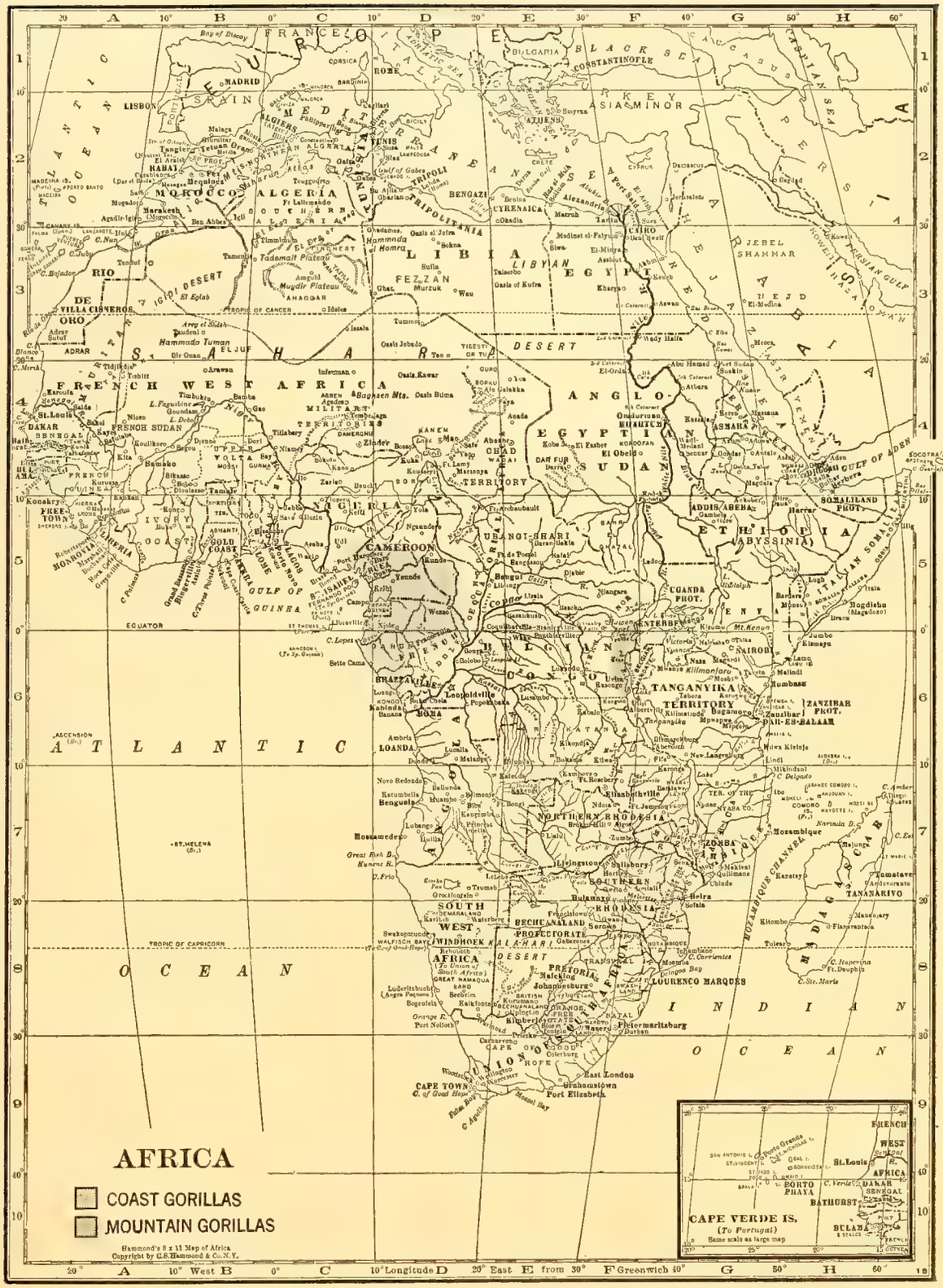
Outline map of Africa. The two shaded areas show regions where gorillas are found. Westernmost, the Coast Gorilla; easternmost, the Mountain Gorilla.


15°
25°
NIGERIA
CAMEROONS
FRENCH
EQUATORIAL
AFRICA
Gabon
BELGIAN CONGO
ANGLO-EGYPTIAN
SUDAN
UGANDA
RUANDA
URUNDI
TANGANYIKA
TERR.
ANGOLA
NORTHERN RHODESIA
Bight of Biafra
Equator
0
10
CENTRAL AFRICA
COAST GORILLAS
MOUNTAIN GORILLAS

MAP 2.

MAP 2.

Equatorial Africa. The shaded area shows the general range of the genus Gorilla so far as it is at present known. The western section includes Gaboon, Cameroons and some of French Equatorial Africa. Here *Gorilla gorilla gorilla* is found. The eastern section includes the Kivu Volcanoes and the highlands of the eastern Congo. Here *Gorilla gorilla beringei* is found.



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